SMALL-SCALE VARIABILITY IN BENTHIC FOOD WEBS IN THE NORTHEASTERN CHUKCHI SEA

By

Kelley L. Tu

RECOMMENDED:

Dr. Larissa Horstmann-Dehn, Ph.D.

Dr. Katrin Iken, Ph.D.

Dr. Arny Blanchard, Ph.D.
Advisory Committee Chair

Dr. Brenda Konar, Ph.D.
Head, Program, Marine Science and Limnology

APPROVED:

Dr. Michael Castellini, Ph.D.
Dean, School of Fisheries and Ocean Sciences

Dr. John Eichelberger, Ph.D.
Dean of the Graduate School

8/20/2013
Date

SMALL-SCALE VARIABILITY IN BENTHIC FOOD WEBS IN THE NORTHEASTERN CHUKCHI SEA

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Kelley Lannon Tu, B.A.

Fairbanks, Alaska

August 2013

Abstract

Benthic food web structure can differ over large scales across Arctic shelves in relation to hydrographic conditions, but little is known if such differences also may occur on smaller scales in hydrographically complex areas. The length, food sources, trophic composition, and energy distribution of benthic food webs in three study areas in the northeastern Chukchi Sea (i.e., Klondike, Burger, and Statoil, as part of the Chukchi Sea Environmental Studies Program) were compared using stable isotope analysis and bomb calorimetry. Food web length (four trophic levels), food sources, and linear models of food webs were comparable among areas. Marked differences in food web structure were observed when trophic levels were quantified by benthic biomass and abundance. High proportions of biomass and abundance of trophic level 3 taxa at Burger were attributed to high deposition of refractory material. High proportions of trophic level 1 and 2 taxa at Klondike and Statoil reflected availability of fresh material. Burger could potentially present a rich foraging ground for some benthic predators due to especially high benthic prey energy densities. Findings emphasize that marine food webs can vary on small spatial scales in accordance with hydrographic conditions, particularly when quantitative trophic level distribution is considered.

Table of Contents

Page

List of Figures

Page

List of Tables

Page

Acknowledgments

First, I would like to thank my advisor, Dr. Arny Blanchard, and my committee members Dr. Lara Horstmann-Dehn and Dr. Katrin Iken. Their advice, guidance, and support have been invaluable through the past few years.

I would also like to thank everyone involved with the Chukchi Sea Environmental Studies Program. I am very grateful to the captain and crew of the M/V *Westward Wind*, the chief scientists and science crews, Aldrich Offshore Services, and Olgoonik-Fairweather LLC, as well as Adrian Gall of ABR, Inc., who provided information on seabirds. Thank you to the 2009–2011 Benthic Field Teams and Jenn Questel, University of Alaska Fairbanks, whose work made the collection of samples for this project possible.

In addition, there are all the members of the University of Alaska Fairbanks Benthic Lab who helped with this research. I would like to express special gratitude to Kevin Fraley, Hilary Nichols, Tama Rucker, Shona Snater, Eric Wood, and Ann Knowlton. I am also very grateful to Tim Howe and Norma Haubenstock at the Alaska Stable Isotope Facility for their assistance.

Thank you to all of my friends in Fairbanks, back east, and in New Zealand. You all have been a constant source of inspiration and optimism, especially when times were rough.

And finally, thank you to mom and dad for letting me spread my wings and fly—even though it meant flying as far as I possibly could without leaving the country.

This work was funded by ConocoPhillips Alaska, Anchorage, AK; Shell Exploration and Production Company, Anchorage, AK; and Statoil USA E&P, Inc., Anchorage, AK. The conclusions herein are mine and do not necessarily represent the views of those companies.

Dedication Page

This thesis is dedicated to Laurie G. Miller and Sampson H. Tu.

SMALL-SCALE VARIABILITY IN BENTHIC FOOD WEBS IN THE NORTHEASTERN CHUKCHI SEA[1]

INTRODUCTION

The abundant and biomass-rich benthic communities in the northeastern Chukchi Sea are an important link between seasonal pelagic and sea ice-associated production and higher trophic level consumers (Bluhm & Gradinger 2008, Grebmeier 2012). The structure of the benthic food web, e.g., number of trophic levels determining length, distribution of feeding guilds, and energy content of benthic food web members, determines much of the energy distribution of the benthic communities on the Arctic shelves. These food web characteristics are known to vary on large regional scales in the Chukchi Sea, due in part to different water mass characteristics and nutrient regimes (Dunton et al. 1989, Iken et al. 2010, Feder et al. 2011). For example, identical consumers fed on a lower trophic level in the nutrient-rich Anadyr Water (AW) compared to the less nutrient-rich Alaskan Coastal Water (ACW) in the southern Chukchi Sea, indicating more direct pelagic-benthic coupling under AW conditions (Iken et al. 2010). The overall stable spatial location of regional-scale water masses and their hydrographic characteristics likely maintains these benthic food web differences. It is currently unknown if such patterns in benthic food web characteristics may be downscaled to smaller spatial scales (Piepenburg 2005). Possibly, advective processes over small scales may prohibit the establishment of distinct benthic food webs or energy

[1] Tu, Kelley L., 2013. Small-scale variability in benthic food webs in the northeastern Chukchi Sea. Prepared for submission in Marine Ecology Progress Series.

hotspots. Alternatively, such small-scale differences may exist due to geomorphological variations and hydrodynamic processes and be of importance to higher-trophic level consumers (Desrosiers et al. 2000, Dunton et al. 2005, Dubois et al. 2007). The purpose of this study was, therefore, to assess if differences in benthic food web characteristics are detectable over small spatial scales in a hydrographically and topographically diverse region of the northeastern Chukchi Sea. Small-scale comparisons in this study are defined as spatial comparisons between 60 km and 120 km (each study area has a total area of ~3,000 km^2 and sampling locations are separated by a few to tens of kilometers). This range is smaller than that of comparisons made by previous studies in the Chukchi Sea (Iken et al. 2010, Feder et al. 2011), which are considered large-scale in this study (total area sampled is up to ~70,000 km^2 with sampling locations separated by tens to hundreds of kilometers).

Benthic food webs in the Chukchi Sea are characterized by tight pelagic-benthic coupling and highly influenced by sea ice dynamics (Dunton et al. 1989, 2005, Grebmeier & McRoy 1989, Grebmeier et al. 1989, Iken et al. 2010). The northeastern Chukchi Sea is seasonally ice covered, approximately six months out of the year (Mysak & Manak 1989, Weingartner et al. 2005, Woodgate et al. 2005). Timing of ice melt affects sympagic and pelagic production (Grebmeier et al. 2006); melting releases ice algae early in the spring, and the subsequent salinity stratification enables formation of a phytoplankton bloom (Sakshaug 2004, Grebmeier 2012). The majority of water column production occurs from late spring through late summer after sea ice has moved out of the region (Grebmeier et al. 2006). Large zooplankton grazers are absent from the

shallow water depths on the shelf in winter/early spring and must be advected into the area from the south (i.e., Bering Sea), resulting in a mismatch between early seasonal production and zooplankton community development (Questel et al. 2013). Consequently, much of the sea ice algae and seasonal production released earlier in the season sinks to the benthos before zooplankton communities develop (Walsh & McRoy 1986, Grebmeier & Barry 1991, Ambrose et al. 2005). The high standing benthic stock on the Chukchi shelf (averaging 5–15 g carbon m^{-2}, but with values as high as 100 g carbon m^{-2} at the head of Barrow Canyon; Grebmeier et al. 2006) is attributed to the flux of ungrazed particulate organic matter (POM) to the bottom and advection of carbon from the highly productive northern Bering and southern Chukchi seas (Dunton et al. 2005, Grebmeier et al. 2006, Feder et al. 2007, Woodgate et al. 2010, Blanchard et al. 2013a, b). The rich benthic communities of the northeastern Chukchi Sea support high densities of upper trophic level benthic predators, such as bearded seals (*Erignathus barbatus*), Pacific walruses (*Odobenus rosmarus divergens*), and gray whales (*Eschrichtius robustus*) (Lowry et al. 1980, Fay 1982, Dehn et al. 2007, Sheffield & Grebmeier 2009).

Stable carbon and nitrogen isotopes are frequently used in food web studies to determine food sources and trophic position of taxa. The stable carbon isotope ratio of primary producers varies according to different photosynthetic pathways, and has a low fractionation with trophic transfer (<1‰; DeNiro & Epstein 1978, 1981, Peterson & Fry 1987, Post 2002). Terrestrial material is more depleted in ^{13}C than marine-derived production. For example, terrestrial material from river inflow into the southern Chukchi

Sea has a $\delta^{13}C$ value of -27‰, and typical marine pelagic primary production $\delta^{13}C$ values fall between -26‰ and -21‰ (Naidu et al. 2000, Gradinger 2009). Stable carbon isotope ratios are, therefore, good indicators of food sources and their origin. Conversely, stable nitrogen isotope ratios have higher fractionation with trophic transfers (~3.4‰ for lower trophic levels; Minagawa & Wada 1984, Peterson & Fry 1987, Post 2002), and are good indicators of trophic position. Processing of the POM food source can also be inferred from stable nitrogen isotope ratios, as microbial degradation results in the loss of the lighter isotope and will leave material isotopically enriched (Altabet & McCarthy 1985, Checkley & Entzeroth 1985, Freudenthal et al. 2001).

The strength of pelagic-benthic coupling in the Chukchi Sea has been evidenced by previous studies with the aid of stable isotope analysis. Benthic food webs in the southern Chukchi Sea are influenced by multiple water masses, including AW and ACW. Each carries different food sources, with marine primary production in the water column offshore (AW) and greater proportions of terrestrial carbon inshore (ACW) (Grebmeier et al. 2006, Iken et al. 2010). High proportions of consumer species within the first trophic level and biomass dominants at low trophic levels indicate a tight pelagic-benthic coupling for the benthic community under AW (Iken et al. 2010). Tight pelagic-benthic coupling in the eastern Chukchi Sea food web between Cape Lisburne and Wainwright is reflected in the low stable carbon isotope variability among consumer feeding groups (~2‰; Dunton et al. 1989). Stable carbon isotope ranges of benthos from the southeastern Chukchi Sea below Cape Lisburne are, however, larger (6.3‰ on the southeastern Chukchi Shelf, and 5.2‰ in the Chukchi Bight) due to increased terrestrial

input into the food webs of these areas (Feder et al. 2011). The benthic system in the northeastern Chukchi Sea is divided into a trophic guild that relies mostly on pelagic production and a trophic guild that also assimilates a non-pelagic carbon source (McTigue et al. 2012).

While benthic food web investigations using stable isotopes are useful for qualitatively examining trophodynamics and pelagic-benthic coupling, energy assessments of benthic prey can expand this information by quantifying the amount of energy deposited to the benthos that is then available to top predators such as marine mammals and seabirds. The caloric content of a local benthic community is largely determined by the energy available through primary production delivered to the system as well as the taxon and feeding type composition of the community. Currents and changes in water circulation due to topographic variations can cause increased availability of POM through advection processes, or increased deposition of POM where water movements are slow (Snelgrove & Butman 1994, Blanchard et al. 2013a, b). Such depositional areas are typically characterized by finer sediments and higher proportions of deposit-feeding organisms (Rhoads & Young 1970, Grebmeier 1993). In contrast, coarser sediments and greater proportions of suspension-feeding organisms are found where water currents are stronger (Feder et al. 1994a, 2005, 2007, Bluhm et al. 2009). These differences in particle flow and feeding types translate into the energy density within the benthic community (Bagatini et al. 2010).

Benthic energy density information can be useful to estimate the potential value of a particular area as a foraging ground for top level predators, the capacity of top level

predators it can support, and the specific energetic impact this predation has on a benthic community (Wesławski et al. 2006). Caloric data can also provide insight on prey quality, which is spatially and temporally variable and affects reproduction and population dynamics of marine mammal predators and seabirds (Rosen & Trites 2000, Trites & Donnelly 2003, Österblom et al. 2008). Tracking changes of the benthic community food web and energy composition due to continued climatic warming or local anthropogenic influences may give insight into effects on marine mammal populations relying on the benthos, as benthic prey abundance, quality, and energy density may have an impact on predator densities (Darling et al. 1998, Piepenburg 2005, Bluhm & Gradinger 2008).

In light of increased management needs due to increased anthropogenic activities in the northeastern Chukchi Sea, the understanding of small-scale variation in benthic food web structure, energy flow, and energy density as hotspots for benthic-feeding top predators becomes a pressing issue. From an ecosystem standpoint, the question is if some of the established large-scale patterns in benthic food web and energy distribution patterns across the Chukchi Sea shelf (Dunton et al. 1989, Iken et al. 2010, Feder et al. 2011, McTigue et al. 2012) are homogeneous, or if in actuality they are a mosaic of small-scale patches that differ in energy flow and benthic food web and energy structure. The Chukchi Sea Environmental Studies Program (CSESP), a multi-disciplinary research project in the hydrographically and topographically complex northeastern Chukchi Sea, afforded the opportunity to assess small-scale variation of food web and energy density structure. The hypothesis tested here was that the benthic food web in the study region

will vary spatially in food source characteristics, food web length, and trophic composition, and that the resulting benthic communities will differ in energy density.

METHODS

Study Area

The overall study region is located off the northwestern coast of Alaska, southwest of Hanna Shoal, between Barrow Canyon and the Chukchi Sea Central Channel (Fig. 1). The study region is 100 to 200 km northwest of the coastal community of Wainwright, Alaska, and contains three study areas: Klondike, Burger, and Statoil. In all three areas successful lease bids for oil and gas development were made during the February 2008 Chukchi Sea Lease Sale 193. Each study area is about 3000 km^2 with Klondike approximately 14 km southwest of Burger, and Statoil northwest adjacent to Burger, where they share a border.

One of the primary water masses affecting the northeastern Chukchi Sea (Bering Shelf Water, BSW) flows north through the Bering Strait transporting heat, carbon, nutrients, oxygen, primary production, and biota into the Chukchi Sea from the south (Weingartner et al. 1998, 2005). Part of the BSW flows north through the Central Channel before reaching the study region. Topographical features, such as the Central Channel and Hanna Shoal (see Fig. 1), play an important role in modifying water mass movement and influencing environmental and biological characteristics of each study area (Winsor & Chapman 2004, Blanchard et al. 2013a). Hanna Shoal, just north of the study region, is approximately 100 km in diameter, and rises 10–20 m above its

surroundings (Martin & Drucker 1997). A portion of the BSW flows north through the Central Channel and branches to the east over Klondike, while the remainder continues to travel north over western Statoil and along the western flank of Hanna Shoal (Fig. 1) (Weingartner et al. 2013). This water travels northward before recirculating into the study region by wrapping around Hanna Shoal in an anticyclonic gyre (Martin & Drucker 1997, Winsor & Chapman 2004, Spall 2007). Circulation models indicate that the recirculating water converges over Burger with the previously mentioned eastward moving currents from Klondike, and the interaction likely creates an area of slowed water movement. While no current velocity readings exist for this area of convergence, the eastward water movement crosses Burger at 2 cm s^{-1} (Weingartner et al. 2013), resulting in fine bottom sediments. Faster currents over Klondike (4 cm s^{-1}; Weingartner et al. 2013) carry away finer bottom sediment fractions and leave coarser grain sizes, resulting in lower organic carbon (OC), mud content, and benthic biomass and abundance compared to Burger and Statoil (Blanchard et al. 2013a). Subtle differences in environmental characteristics also exist between Burger and Statoil, though these two areas are overall similar; Statoil is slightly shallower, with lower OC and coarser sediments, while increased water depths exist at Burger at the head of a submerged watershed draining towards Barrow Canyon (Blanchard et al. 2013a). The described topographic and circulation patterns create an environmental gradient that spans from a more dynamic habitat in the south (Klondike) to a more depositional environment in the northern study areas (Burger and Statoil) over a relatively small spatial scale. Despite similar overall benthic faunal composition among all areas (Blanchard et al. 2013a), seabird and marine mammal observations suggest that

Klondike is a more pelagic-driven system, while Burger is more of a benthic-driven system. For example, densities of fishes and planktivorous seabirds are higher at Klondike than Burger, where benthic-feeding marine mammals occur in higher densities and where benthic biomass and density are higher (Aerts et al. 2013, Blanchard et al. 2013a, Day et al. 2013, Gall et al. 2013). Statoil shares biological characteristics with both of the other study areas.

Sample collection and preparation

Sampling for this study occurred annually from 2009–2011 at Klondike, Burger, and Statoil (2010 and 2011 only) at a total of 76 stations. However, not all sample types were collected every year and at every station. Samples were collected from 17 August to 10 October 2009, and 5 August to 14 September 2010 and 2011. Four sample types were collected: sediments, benthic invertebrates, POM, and benthic energy content (Fig. 2).

POM and surface sediments were sampled to characterize the food sources available to the benthic food web. POM from the chlorophyll maximum layer (5 m to 43 m above the seafloor) was sampled using Niskin bottles on a Seabird SBE25/SBE55 CTD (conductivity-temperature-depth) rosette from 1–20 September 2010, with one replicate per station. Fifty ml of water was filtered under low pressure onto a Whatman GF/F filter (0.7 μm) and frozen for stable isotope analysis (Parsons et al. 1984). All frozen samples were kept at -4˚C aboard the vessel. The top 5 cm of sediment from one side of a 0.1 m^2 double van Veen grab was collected into 50 ml centrifuge tubes and

frozen for stable isotope analysis during the 2009–2010 cruises, with one replicate per station.

Invertebrate samples were collected during all cruises. Epifauna were collected with a 3.05-m plumb staff beam trawl (4-mm codend liner, 7-mm mesh) during the 2009–2010 cruises from eight stations at Klondike, 12 stations at Burger, and one station at Statoil. Epifauna were sorted, identified to the lowest taxonomic level possible, and frozen in individual Whirlpak™ bags by taxon for stable isotope analysis and bomb calorimetry. Infaunal samples were collected from one side of a 0.1 m^2 double van Veen grab during the 2009–2011 cruises from 14 stations each at Klondike and Burger, and 26 stations from Statoil. Grabs were rinsed through 1-mm mesh screens, invertebrate taxa collected, and frozen for stable isotope analysis and bomb calorimetry. Whole organisms (infaunal and epifaunal) were partially thawed in the laboratory, identified to the lowest taxonomic level possible, rinsed with deionized water to remove debris, and then freeze-dried. Polychaetes of the family Maldanidae and the bivalve *Ennucula tenuis* (each n=3 where possible), and other infaunal taxa (1–6 replicates per station) representative of common fauna in the Chukchi Sea as found by other studies (Feder et al. 2005, 2011, Iken et al. 2010), were selected for stable carbon and nitrogen isotope analysis. A total of 92 taxa were analyzed, consisting of 46 infaunal and 46 epifaunal taxa.

Stable isotope analysis

POM filters were oven-dried at 60˚C for 24 h and acid-fumed for 48 h with HCl vapors in a vacuum chamber for removal of carbonates (Iken et al. 2010), which affect

stable carbon isotope signatures. One third to one half of the top layer of the filter was scraped off and weighed into tin capsules. Sediments were rinsed in 1 N HCl until bubbling ceased, rinsed with deionized water, freeze-dried on a VirTis Sentry freeze dryer, and weighed (13–17 mg) into tin capsules for stable carbon and nitrogen isotope analysis.

Differences in tissue turnover rates can bias stable isotope measurements (Peterson & Fry 1987). Therefore, benthic invertebrate samples were prepared using whole body homogenates, including shells, to obtain an average stable isotope signature for the organism (McClelland et al. 1997, Anderson & Polis 1998, Michener & Kaufman 2007). Samples were acidified and lipid-extracted to remove bias of ^{13}C-depleted carbonates and lipids, respectively, on δ^{13}C measurements (DeNiro & Epstein 1978). Samples were acidified with 1 N HCl for removal of carbonates (Dunton et al. 1989, Iken et al. 2010). Samples were freeze-dried, and then lipid-extracted with a minimum of three 24 h soaks in 5 mL of 2:1 chloroform methanol (Folch et al. 1957, Post & Parkinson 2001, Hobson et al. 2002, Arrington et al. 2006). As a caveat, lipid-extraction can affect stable nitrogen isotope signatures (Sotiropoulos et al. 2004, Logan et al. 2008), which will need to be considered when comparing δ^{15}N results to other studies. Samples were freeze-dried for a minimum of 24 h after solvent removal. Multiple individuals were composited when organisms were too small to provide at least 5 mg of material for stable isotope processing (to account for loss of material during processing). Samples large enough to yield sufficient mass were homogenized with mortar and pestle prior to processing, otherwise they were processed whole. A 0.1–0.5 mg subsample from each

homogenized sample was weighed into tin capsules for stable carbon and nitrogen isotope analysis.

Samples were analyzed for stable carbon and nitrogen isotopes at the Alaska Stable Isotope Facility (University of Alaska Fairbanks). All analyses were performed using a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer with Pee-Dee Belemnite (PDB) and atmospheric nitrogen (N_2) as standards for stable carbon and nitrogen isotope measurements, respectively. Sample isotope ratios are expressed in standard δ notation in parts per thousand (‰) using the equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000 \quad (1)$$

where X is ^{13}C or ^{15}N, and R is the corresponding isotopic ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Instrument error was determined by a laboratory peptone standard (Ben-David & Flaherty 2012). Analytical instrument error was ±0.10‰ for $\delta^{13}C$ and ±0.18‰ for $\delta^{15}N$ (n=144 each). Trophic levels were calculated based on primary consumer $\delta^{15}N$ values using the following formula:

$$TL_{(PC)} = (\delta^{15}N_{consumer} - \delta^{15}N_{primary\ consumer}) / 3.4 + 2 \quad (2)$$

where $TL_{(PC)}$ is the calculated trophic level based on a primary consumer (PC), and 3.4‰ is the average enrichment among trophic levels for aquatic consumers (Minagawa & Wada 1984, Vander Zanden & Rasmussen 2001, Post 2002, Iken et al. 2010). Trophic

level calculations were based on a primary consumer (the amphipod *Ampelisca eschrichti*) rather than POM, as the POM source is temporally and spatially variable, while primary consumers present a time-integrated measure of local primary production (Post 2002). To quantify the community distribution within trophic levels, biomass (g m^{-2}) and abundance (individuals m^{-2}) data from 2009–2011 of the macro- and megafaunal community (Blanchard et al. 2013a, b) were averaged for each of the three study areas by taxon and binned by trophic level. Although some interannual differences in biomass and abundance existed in each area, averaging across years was considered appropriate to answer the research question of small-scale variability of this study, which was not concerned with temporal variation. Nevertheless, averaging these values likely added a low to moderate amount of variation based on the standard deviations calculated for the benthic communities over the three years (Table 1). POM and sediment C/N ratios were calculated based on the weight-to-weight percent of C and N provided with stable isotope measurements and were used to determine nutritional quality, with lower C/N ratios indicating higher nutritional quality (Gnaiger & Bitterlich 1984, Dorgelo & Leonards 2001). POM and deposited surface sediments are generally composed of detrital material, which consists of senescent algae, plant material, and faecal pellets (Valiela 1995). Therefore, a high C/N ratio would likely indicate presence of terrestrial or refractory carbon such as cellulose (Walsh 1980). A low C/N ratio suggests higher food quality due to greater presence of microbial proteins and less refractory material (Parsons et al. 1984, Taylor & Roff 1984). Animals were categorized by feeding type based on known feeding methods (Young & Rhoads 1971, Taylor 1978, Fauchald & Jumars 1979, Rice et al.

1980, Coyle & Highsmith 1994, Feder et al. 1994b, 2007, 2011, Holte & Gulliksen 1998, Oug 2000, Iken et al. 2005, Kędra & Murina 2007).

Bomb calorimetry

Forty-seven infaunal and epifaunal taxa from the study region were selected for bomb calorimetry analysis, on the basis that they are known prey items of Arctic pinnipeds and cetaceans (Lowry et al. 1980, Fay 1982, Darling et al. 1998, Pauly et al. 1998, Sheffield et al. 2001, Dehn et al. 2007, Sheffield & Grebmeier 2009, Quakenbush et al. 2011a, b). Prey of benthic-feeding seabirds were excluded from analyses because benthic-feeding species were rarely sighted in the study areas (<1% of records; Gall personal communication). The relatively large amount of material needed for calorimetry and prevalence of epibenthic prey items in many marine mammal diets restricted taxon selection mostly to those collected from trawls. Limited spatial coverage of trawls prohibited study area comparisons of caloric data within taxa; therefore, mean caloric content for a taxon was extrapolated for all areas or averaged across study areas if several collections existed. Only taxa collected in 2009 were selected for bomb calorimetry to exclude temporal variability in caloric content. For caloric processing, shells were removed from gastropods and bivalves as soft body parts are extracted from shells during consumption by marine mammals. Invertebrates with inorganic structures that were difficult to separate from tissue (e.g., echinoderms, decapods) were homogenized and analyzed whole. These types of prey are being consumed whole by marine mammal predators, therefore this method better approximates energy gained by ingestion. Multiple

animals were pooled where individuals did not provide sufficient mass for analysis. Pooled samples consisted of individuals collected from the same station. Wet mass (WM) was recorded, and samples were frozen before freeze-drying for a minimum of 48 h. Dry mass (DM) was recorded following lyophilization (for wet weight to dry weight conversion factors) and samples were homogenized with mortar and pestle. Dried samples were formed into pellets (~0.5–1 g) and analyzed on a Parr model 6300 oxygen bomb calorimeter for gross energy content at the Marine Mammal Laboratory (University of Alaska Fairbanks). Samples that did not hold their form in a pellet were analyzed in gelatin capsules. Five empty gelatin capsules were weighed and analyzed to determine their average caloric value for correction of prey caloric content (2.06 kJ per capsule). Instrument error (±0.04 kJ g^{-1}) was determined by analysis of 12 benzoic acid standards (Parr Instrument Co.). Replicates on pooled and individual taxa were run as many times as the amount of available sample would allow (2–10 times). Mean caloric content of taxa is reported in kJ g^{-1} DM and kJ g^{-1} WM. Caloric values based on WM were used to generate the energy density kriging plots as DM measurements do not accurately represent the energy gained by consumption of live prey.

Statistical analyses

Statistical analyses were performed using the software package R (www.r-project.org, V2.15.0). Data were normally distributed and no transformation was required. To assess if sediment data from two collection years could be combined, an ANOVA (analysis of variance, $\alpha = 0.05$) was used to determine if interannual differences

existed. Statoil sediment data were excluded from this as there were only data collected from 2010. One-way ANOVA was used to compare sediment and POM stable carbon and nitrogen isotope values (pooled over years), and energy densities among the three study areas, followed by Tukey's post hoc test for multiple comparisons. Simple linear regression has traditionally been used to model the correlation between stable carbon and nitrogen isotopes in marine food webs (Mincks et al. 2008, Fanelli et al. 2009, Feder et al. 2011, Kędra et al. 2012). However, the use of $\delta^{13}C$ as a quantitative predictor violates the assumption of a fixed predictor in simple linear regressions (Quinn & Keough 2002). Therefore, regressions of isotope data by area were performed using Model II regression (ranged major axis regression, RMA regression) for two random variables to account for the use of measured stable carbon isotope values in the regression models (Laws & Archie 1981, Quinn & Keough 2002). In this study, RMA regression considered $\delta^{13}C$ as the quantitative predictor and $\delta^{15}N$ as the response. RMA regression methods are defined for regression with one predictor variable; therefore, a "Study Area Effect" was determined by comparing confidence intervals of regression coefficients. Significant differences were determined by lack of overlap of 95% confidence intervals (Laws & Archie 1981). Geospatial modeling was performed using the library geoR for R. Kriging plots modeling prey energy density (kJ WM m^{-2}) in each study area were generated using caloric content (kJ g^{-1} WM) and biomass data (Blanchard et al. 2013a, b) of marine mammal prey items previously identified from stomach contents (Lowry et al. 1980, Fay 1982, Pauly et al. 1998, Sheffield et al. 2001, Dehn et al. 2007, Sheffield & Grebmeier 2009, Quakenbush et al. 2011a, b).

RESULTS

Stable isotope analysis

POM from Klondike stations were significantly more ^{13}C-enriched compared to Burger and Statoil ($p < 0.001$) with the latter two being statistically similar ($p = 0.891$) (Tables 2 and 3). There was no significant difference among areas for POM $\delta^{15}N$ (ANOVA, $p = 0.332$) or C/N values (ANOVA, $p = 0.150$) (Table 2). Average POM C/N ratios by study area ranged from 6.24–6.70.

There were no significant differences among years or year by study area interactions within Klondike and Burger sediment data for $\delta^{13}C$, $\delta^{15}N$, or C/N (all $p \geq 0.196$) (Table 2), allowing interannual data to be combined per area. Sediment stable carbon and nitrogen isotope values were significantly different among study areas (Table 2). Sediment $\delta^{13}C$ was significantly lower at Klondike compared with Statoil ($p < 0.001$), and $\delta^{15}N$ was significantly lower at Klondike compared with Burger ($p = 0.001$) (Table 2). Sediment C/N ratios differed significantly (ANOVA, $p < 0.001$), with Klondike sediments having a higher C/N ratio than both Burger and Statoil ($p = 0.019$, $p < 0.001$, respectively) (Table 2). POM from stations in Klondike was relatively more ^{13}C- and ^{15}N-enriched than Klondike sediments, whereas POM was ^{13}C-depleted and ^{15}N-enriched compared with sediments at stations in Burger and Statoil (Table 3).

A total of 112 taxa were analyzed for stable carbon and nitrogen isotopes with approximately 50 taxa from each study area (Table 3). The 95% confidence intervals for the intercepts and slopes from RMA regressions overlapped in range, indicating no

difference in stable isotope correlations among study areas (Table 4). The fitted linear models of food webs were similar among areas, indicating similar food web structures among areas (Fig. 3).

The food webs spanned four trophic levels from POM to higher-order benthic predators such as predatory gastropods and polychaetes for all study areas (Table 3). Proportional contributions of biomass and abundance to trophic levels by area showed the highest proportions of both quantitative measures within trophic level 3 at Burger (dominated in biomass by *Ophiura sarsii*, and by *Maldane sarsi* in abundance), while Klondike and Statoil exhibited higher proportions of biomass and abundance at trophic level 2 (high proportions of bivalves) (Fig. 4). Stable carbon and nitrogen isotope values were compared for four taxa that were collected in all three study areas to examine spatial variation within taxa; these four taxa showed similar stable carbon and nitrogen isotope positions in all areas (Fig. 5). However, Ampeliscidae from Klondike and *Anonyx* spp. from Statoil were more enriched in ^{13}C than the respective taxa at the other study areas.

Benthic energy content

A total of 47 taxa collected in 2009 were analyzed for gross caloric content across the study region (Table 5). Average energy density by study area was 477 kJ WM m^{-2}, 747 kJ WM m^{-2}, and 595 kJ WM m^{-2} for Klondike, Burger, and Statoil, respectively. Burger had significantly higher energy density than Klondike ($p = 0.012$), but was not statistically different from Statoil ($p = 0.229$) (Table 6). Kriging plots of energy density showed an increasing west-east gradient across each study area in 2009 (Fig. 6). This

trend was particularly strong at Burger and Statoil, ending in an area of peak energy density at the eastern edges of these areas. Projected west to east energy density ranged from 640 kJ WM m^{-2} to 760 kJ WM m^{-2} in Burger, and from 520 kJ WM m^{-2} to 760 kJ WM m^{-2} in Statoil. Klondike energy density was relatively constant across the study area, ranging from 500 kJ WM m^{-2} to 540 kJ WM m^{-2} (west to east).

DISCUSSION

Small-scale spatial differences among study regions in the POM food source were mirrored in suspension-feeding consumers, possibly linked to differences in local primary production. The sediment detrital pool, however, was similar in all areas. The distribution of benthic biomass and abundance among trophic levels varied by study area, reflecting effects of topographic control of water movement on the deposition of food particles to the benthos. Energy density also varied spatially and suggests that Burger has the most energy-rich benthic community of the three study areas.

Food sources

Sources of carbon for Arctic benthic marine food webs include water column, benthic, ice-edge, and sea-ice production, as well as export from terrestrial and nearshore sources to offshore benthos (Syvertsen 1991, Belicka et al. 2002, Ambrose et al. 2005, Grebmeier et al. 2006, Glud et al. 2009, Gradinger 2009). These POM carbon sources to the benthos are heterogeneous materials that can be spatially and temporally variable (Hill et al. 2005, Gradinger 2009, Iken et al. 2010). The stable carbon isotope signatures

for POM and sediments in the northeastern Chukchi Sea in this study suggest mainly marine carbon sources, which are isotopically heavier than terrestrially derived sources (Naidu et al. 2000). Typical pelagic primary producer $\delta^{13}C$ in the Arctic range from -26‰ to -21‰ (Gradinger 2009), and terrestrial material in the southern Chukchi Sea is estimated to have a $\delta^{13}C$ signature of -27‰ (Naidu et al. 1993). The mean stable carbon isotope ratios of POM in this study were mostly between -21 and -24‰, indicating a food source composed of largely marine carbon with possibly some mixing of more ^{13}C-depleted sources. However, Klondike POM $\delta^{13}C$ values were significantly different from Burger and Statoil. The mean Klondike POM $\delta^{13}C$ value (-21.56‰) more closely reflects marine primary production (Bering Sea phytoplankton $\delta^{13}C$: -21.2 ± 1‰, Naidu et al. 1993), whereas mean Burger POM $\delta^{13}C$ (-23.23‰) and Statoil POM $\delta^{13}C$ (-23.10‰) show more influence from isotopically depleted sources. Low C/N ratios (<6) and high $\delta^{15}N$ values (8‰) are typical of marine POM (Naidu et al. 1993), and coincide with the data presented herein; C/N ratios were ~6 and $\delta^{15}N$ values were within one standard deviation of 8‰ at all study areas. These results suggest that terrestrial material was not present in POM, and that the ^{13}C-depleted source at Burger and Statoil is of marine origin. Linear regression results show that regardless of origin, there are multiple food sources assimilated into the benthic food web. Trophic-shift assumptions of 3.4‰ for nitrogen ($\delta^{15}N$; Vander Zanden & Rasmussen 2001, Post 2002, Mincks et al. 2008, Iken et al. 2010, Kędra et al. 2012) and 0.6‰ for carbon ($\delta^{13}C$; Søreide et al. 2006) provide a theoretical slope of approximately 5.67 ($\delta^{15}N$/ $\delta^{13}C$) for a single food source predatory

food chain (Mincks et al. 2008). When there are multiple food sources with different stable isotope signatures, the fitted model's slope will diverge from the theoretical value, or the model will become nonlinear (Feder et al. 2011). The slope coefficient (β_{RMA}) and 95% confidence intervals of the RMA regression fitted linear models for each study area fell below the theoretical slope, suggesting the presence of multiple carbon sources (β_{RMA}= 1.69–2.17) (Table 4).

Seasonal ice and water movement patterns can affect phytoplankton composition in blooms and POM $\delta^{13}C$ values. The summer progression of ice retreat and water mass movement in the study region may account for the difference in POM $\delta^{13}C$ values between Klondike and the other study areas. Ice cover loss and stratification enable a spring phytoplankton bloom, which follows the retreating ice edge (Hill & Cota 2005, Wang et al. 2005). The seasonal ice retreat pattern in the study region is south to north (Weingartner et al. 2013); therefore, the spring bloom following break up typically begins in Klondike and reaches Statoil and Burger later. Summer water mass movement into the region follows a similar progression. BSW gradually expands east into the study region from the Central Channel and replaces cold, saline winter water (WW, from salt expulsion during ice formation) and surface meltwater (MW, from ice melt) (Day et al. 2013, Weingartner et al. 2013). BSW moves first into Klondike, then Statoil, and then Burger approximately 4–6 weeks later (Day et al. 2013, Weingartner et al. 2013). The timescale of the spring bloom is, therefore, delayed from Klondike to Statoil to Burger due to this seasonal water movement, which has implications for POM $\delta^{13}C$ signatures. Phytoplankton cell size and growth rate can affect POM stable carbon isotope signatures

because larger, fast growing cells in early stages of a bloom are typically more enriched in ^{13}C compared with smaller, slower growing cells at late stages of a bloom (Fry & Wainright 1991, Korb et al. 1996, Burkhardt et al. 1999, Tamelander et al. 2009). $\delta^{13}C$ signatures can also vary among marine phytoplankton species (Falkowski 1991, Kopczyńska et al. 1995). Phytoplankton assemblages were not analyzed in this study, but later ice retreat and delayed flushing of WW over Burger and Statoil may cause a difference in bloom stage and phytoplankton composition in these areas compared with Klondike. This could be a mechanism behind the observed differences in POM $\delta^{13}C$ values.

Stable carbon isotope signatures of consumers can provide insight on the timescales of variability in food sources if tissue turnover rates are known. Spatial differences in ^{13}C enrichment also were observed in the amphipods of the family Ampeliscidae, which had higher $\delta^{13}C$ values at Klondike than those collected from Burger and Statoil (Fig. 5). Primary consumers, such as suspension-feeding ampeliscids, are linked directly to available carbon sources in an area, and their $\delta^{13}C$ signatures represent an average of local food source $\delta^{13}C$ signatures (DeNiro & Epstein 1978, Fry 1988, Saupe et al. 1989). Benthic invertebrates integrate the stable isotope signature of their diet on the order of weeks to months (McMahon et al. 2006, Kaufman et al. 2008, Weems et al. 2012), as opposed to POM, which represent the immediately available material and can change in a matter of days. Stable carbon isotopes have a half-life of ~20 days in Arctic amphipods (Kaufman et al. 2008), indicating that the observed POM differences among areas may have been present for several weeks and alluding to

possible small-scale spatial variation in food sources. However, the mean $\delta^{13}C$ values of deposit-feeding consumers (*Ennucula tenuis* bivalves and Maldanidae polychaetes) in the three study areas were within a 1‰ range of each other (Fig. 5). These animals reflect spatial variation in deposited food sources instead of suspended matter due to their sedentary nature and feeding habits. Mean sediment $\delta^{13}C$ values were significantly different within 0.5‰ in all areas, but observed differences were likely not ecologically significant. The lack of a strong spatial pattern in sediment and deposit-feeding taxa indicates that despite variability in water column production, sediment microbial activity seems to render the detrital pool overall very similar in all areas.

Microphytobenthos and sea ice algae are two possible food sources to the benthos that were not examined in this study. Microphytobenthos are major contributors of primary production to communities in shallow seas (McMinn et al. 2005) and typically are enriched in $\delta^{13}C$ by ~6‰ over phytoplankton (Herman et al. 2000, Kang et al. 2003). Dense filamentous microalgal mats have been observed in the nearshore Chukchi Sea after ice melt (Matheke and Horner 1974) and recent work in the northeastern Chukchi Sea suggests that microphytobenthos are present and a possible food source to the benthos there (McTigue et al. 2012). The importance of sea ice algae to benthic food webs in this region has not yet been extensively studied. However, substantial amounts of ice algae are released during ice melt in the Chukchi Sea and are a food source to benthic and pelagic organisms (McMahon et al. 2006, Gradinger 2009). Ice algae tend to aggregate and sink quickly out of the water column (Michel et al. 1993, Haecky et al. 1998, Mincks et al. 2008, Lavoie et al. 2009), and, therefore, can accumulate in surface

sediments. Ice algal $\delta^{13}C$ values in the Chukchi/Beaufort seas are highly variable (-25‰ to -14‰) and increase with ice algal biomass during the growing season (Tremblay et al. 2006, Gradinger 2009), leaving them enriched in ^{13}C over phytoplankton. Sediment $\delta^{13}C$ from the study areas were ^{13}C-depleted compared with expected ice algal and microphytobenthos stable carbon isotope signatures. Also, mean sediment chlorophyll-*a* values from 2009 and 2010 were very low (ranging from 0.015–2.554 μg cm^{-3}; Blanchard et al. 2013a). The presence of microphytobenthos or sea ice algae in surface sediments during the time of collection is, therefore, unlikely. However, microphytobenthos and ice algal $\delta^{13}C$ signatures may be detected in primary consumer tissues. In this study, *Ennucula tenuis* $\delta^{13}C$ signatures overlapped with both microphytobenthos and ice algal $\delta^{13}C$ ranges as potential food sources (Fig. 5), suggesting ingestion of an enriched food supply based on the assumed 0.6‰ trophic enrichment factor in $\delta^{13}C$ from source to consumer (DeNiro & Epstein 1978, Søreide et al. 2006). Infaunal sampling began between August 5 and August 17 for all years, approximately 16–28 days following the typical ice free date for the study region during the 2009–2011 sampling seasons (July 20; Weingartner et al. 2013). Feeding experiments have shown that arctic benthos readily consume deposited ice algae within several days and may exhibit preferential feeding on this food source (McMahon et al. 2006, Sun et al. 2007). It is therefore possible that ice algae were deposited earlier in the season during break up (prior to July 20) and consumed and assimilated by *E. tenuis* before sampling occurred. To summarize, these findings support the hypothesis that pelagic food source characteristics vary in the study region, likely due to hydrographic and ice retreat differences among areas. The sediment

detrital pool, however, was comparable among all areas and may be a result of similar microbial activity.

Food web structure

Food web structure is often an indicator of ecosystem functioning; benthic food web length can indicate how tightly trophic levels are coupled to primary production. Quantitative distribution within the community among the trophic levels of a food web shows the major pathways of how the bulk of primary production is assimilated (Iken et al. 2010). Small-scale differences in food web structure among study areas were evaluated by comparing linearity, number of trophic levels, and quantitative contributions of biomass and abundance to trophic levels. The fitted linear models and trophic levels of taxa were similar among areas, and all study areas had four trophic levels (Fig. 3, Table 3). This agrees with the food web length and a detritally-based food web found in other Arctic regions (Hobson et al. 1995, Raffaelli 2000, Iken et al. 2005, 2010, Dunton et al. 2012, Kędra et al. 2012).

The quantitative representations of trophic levels (based on community biomass and abundance) in conjunction with feeding mode information can reflect the delivery processes and nature of primary production supplied to an area. For example, benthic communities in the southern Chukchi Sea under the influence of AW and ACW have the same number of trophic levels; however, communities under AW are quantitatively dominated by lower trophic level fauna (Iken et al. 2010). These animals feed directly on labile carbon, and their strong presence emphasizes the abundant supply of fresh material.

This is in contrast to communities under ACW, which are dominated by higher trophic level deposit feeders utilizing more refractory material with enriched stable nitrogen isotope signatures. A similar pattern was observed in the present study, with communities at Klondike and Statoil showing higher abundance and biomass of trophic level 1 and 2 consumers of labile carbon, whereas Burger was dominated by trophic level 3 nonselective deposit feeders. These differences may be attributed to indirect effects of topographic control of water movement on biological communities (Desrosiers et al. 2000, Blanchard et al. 2013a, b). The presence of Hanna Shoal north of the study region creates an anticyclonic gyre and causes currents to converge and slow over the Burger study area (Weingartner et al. 2013). The slowed water movement results in increased deposition of organic matter (Blanchard et al. 2013a, Weingartner et al. 2013). This high amount of organic matter is then subjected to microbial degradation and deposit-feeding bioturbation, which enrich sediments in ^{15}N through bacterial degradation of amino acids and deamination processes (Freudenthal et al. 2001, Granger et al. 2011). The resulting enrichment in ^{15}N of the deposited food source propagates up the food chain when organic matter, meiofaunal degraders, and microbes are assimilated by nonselective deposit-feeding organisms. For these reasons, depositional areas such as Burger are expected to show a strong presence of higher trophic level detritivores. Conversely, stronger currents at Klondike and Statoil may create more favorable conditions for suspension feeders and other primary consumers by supplying fresh labile material from advection or resuspension. The differences in flow processes and particle deposition vs. suspension appear to strongly influence the major energy pathways through the various

trophic levels. These results suggest that current regimes at Statoil are more similar to those at Klondike than those at Burger, despite the close proximity of Statoil and Burger.

High proportions of primary consumers at lower trophic levels are indicators of tight pelagic-benthic coupling where most of the labile material from primary production is delivered to the benthos (Iken et al. 2010). This condition was observed at Klondike and Statoil. The near absence of trophic level 1 organisms at Burger implies a more refractory energy pathway by nonselective deposit feeders, most likely due to a lack of fresh material. It is also possible that the large number of trophic level 3 Maldanidae polychaetes at Burger (thousands of individuals per m^2) out-compete lower trophic level animals, such as bivalves, for space and food (Levin et al. 1997). Sediment core chlorophyll-*a* analyses show that deposited phytoplankton generally is highest at the surface and declines with depth (Blanchard et al. 2013a), indicating that fresh material is not rapidly subducted out of reach of surface deposit feeders. Organic material that may be stored at depth can also be redistributed back to the surface via bioturbation activities by benthic-feeding predators, especially walruses (Ray et al. 2006). Therefore, food limitation does not seem to explain the absence of surface-feeding bivalves at Burger. However, the competition for space and destabilization of sediments by worm tubes may create an unfavorable habitat that prevents establishment of a substantial bivalve community (Eckman et al. 1981). In summary, these findings support the overall hypothesis that small-scale differences in food web structure exist in the study region. These differences were likely driven by differences in water flow and particle deposition in the different study areas, resulting in varying levels of pelagic-benthic coupling

strength. This caused differences in the composition of benthic feeding types that are most apt at exploiting these particle flux differences (e.g., dominance in suspension-feeding vs. deposit-feeding).

Energy density of benthic communities

Stable isotope analysis indicated that there was strong pelagic-benthic coupling in the study areas; therefore, it was of interest whether this coupling was reflected in the spatial energy distribution of the benthic community. In this study, the eastern side of the study region around Burger exhibited the highest benthic gross energy density values (Fig. 6, Table 6). Landscape features such as canyons and shoals are areas of high benthic production due to focused deposition of sediments and organic matter (Rosenberg 1995, De Leo et al. 2010, Blanchard et al. 2013a, b), which has a direct positive effect on benthic biomass (Grebmeier et al. 1988, Grebmeier & McRoy 1989). Higher benthic biomass at Burger compared with Klondike and Statoil was a contributing factor to the higher gross energy density values at Burger (Blanchard et al. 2013a). However, taxonomic composition of the benthic community also may have an effect on gross energy values due to differences in caloric content of the individual taxa (Atkinson & Wacasey 1983, Wacasey & Atkinson 1987, Lawson et al. 1998, Ball et al. 2007, Hondolero et al. 2012). The small-scale spatial pattern of energy density observed here coincides with the distribution of bivalve biomass, which are abundant at the calorically-rich areas of Statoil and just to the east of Burger (Blanchard et al. 2013a). On a larger spatial scale, the predicted benthic community energy densities in this study are

comparable to or higher than other regions with similar benthic community composition. For example, the mean energy density of benthic and epibenthic invertebrates in St. Margaret's Bay, Nova Scotia, Canada is 318 kJ WM m^{-2}, with a maximum station value of 728 kJ WM m^{-2} (Brawn et al. 1968). This maximum value is similar to the highest station values from this study and the projected mean gross energy density is lower than in the present study. This comparison suggests that the study region is relatively rich in benthic invertebrate prey for higher trophic levels given that other foraging constraints are negligible (e.g., ice cover, depth).

Arctic marine mammal predators feeding on benthos (e.g., walruses, bearded seals, gray whales) will attempt to maximize energetic gain by maximizing quantity and quality of prey ingested and reducing foraging costs, a strategy described by the optimal foraging theory (Emlen 1966, Perry & Pianka 1997, Rosen & Trites 2004, Spitz et al. 2012). Accordingly, marine mammal predators appear to target prey occurring in high densities, or prey having high energy content (summarized by Bluhm & Gradinger 2008). The energy density values calculated here account for between 31% to 98% of total benthic biomass at any given station as these values are only inclusive of benthic invertebrate prey for a select group of benthic-feeding marine mammals (Table 7). Therefore, gross energy density estimates are almost certainly an underestimate of total available prey energy density, which include taxa (e.g., benthic fishes) that may be important prey items, but were not collected in this study. A 550 kg adult female walrus summering in the Chukchi Sea may consume as much as 106,000 kJ per day (193 kJ per kg body mass; Fisher et al. 1992). Taking into consideration a Pacific walrus population

of approximately 129,000 individuals (Speckman et al. 2011), even if only 26% of this population utilize the northeastern Chukchi Sea (based on Gilbert 1989), the potential impact of just this one predator on the benthos is substantial. For example, even in the highest density energy region of the study areas in eastern Burger (approximately 750 kJ WM m^{-2}), a single adult female walrus would have to exploit roughly 140 m^2 of the bottom invertebrate community per day to satisfy its daily energy needs. Therefore, within the small scale of the study region, the eastern parts of Statoil and Burger seem to present better benthic marine mammal feeding grounds compared with Klondike. This is supported by satellite tag and observational data that indicate large aggregations of walruses (as many as 700 individuals) hauled out on ice in the Burger area (Jay et al. 2012, Aerts et al. 2013). However, on the larger, population scale of bottom-feeding mammal predators, the study region overall can only satisfy a small amount of their energy demands. The predation pressure on benthic systems may be alleviated by an extended prey spectrum of some marine mammals. Bearded seals, for example, may feed heavily on pelagic prey during years of reduced sea ice extent (Carroll et al. 2013), which extends their prey list to high-energy taxa (such as pelagic fishes; Ball et al. 2007). Walruses and bearded seals also feed extensively on pelagic and benthic fishes (Antonelis et al. 1994, Quakenbush et al. 2011a), which were not captured in the energy estimates of this study. It is also noteworthy that prey digestibility factors into a predator's prey selection, and that lack of specialized feeding abilities or physiological limitations (e.g., suction-feeding, aerobic dive limit, thermoregulatory costs, diving capabilities) may prevent a predator from consuming a specific prey regardless of its energy quality (Rosen

et al. 2007). For these reasons, consideration of taxonomic composition and physical limitations of the predator is important when drawing inferences of top predator feeding patterns from benthic prey energy density. In addition to the small-scale spatial variation in gross energy density of the benthic invertebrate community determined here, individual prey taxa also may vary temporally based on reproductive status, and temporally varying food availability and food quality (Jorde & Owen 1990, Bagatini et al. 2007, 2010, Leu et al. 2010). Data presented herein, however, are useful as an approximation of the mean caloric content/gross energy density values available for consumption by higher trophic levels during the late summer/early fall in the northeastern Chukchi Sea. These findings support the hypothesis that benthic food webs vary in gross energy density among study areas. This small-scale variability is most likely highly influenced by hydrographic conditions affecting particle deposition.

CONCLUSIONS

Small-scale spatial differences were detected in some benthic food web characteristics among the study areas in the northeastern Chukchi Sea. Marked differences among areas were observed when trophic levels were quantified based on benthic invertebrate biomass, abundance, and energy density. These differences are likely linked to interactions of topography and the overlying water mass currents that increase the particle deposition at Burger. There was a dominance of trophic level 3, nonselective deposit feeders at Burger, indicative of a highly depositional area of refractory material. Water current conditions at Klondike and Statoil appear to be similar and favored

consumers of suspended labile carbon sources, as shown by dominance of trophic level 1 and 2 taxa. The resulting benthic communities differed spatially in energy density, as hypothesized. The findings presented herein show that substantial differences in benthic food webs are detectable in fine resolution studies; these small-scale differences may have important ecological implications, such as delineating rich feeding grounds for marine mammal predators.

One possible scenario of continued climatic warming in the Arctic is a shift of ecosystems towards decreased primary production exported to the benthos through heavier zooplankton grazing, thus favoring a pelagic food web. This can have negative implications for the benthic communities in the study region, possibly to a higher degree in the energy-rich regions of Burger, where high quantities of deposited food structure the benthic community. Results from this study give insight on the spatial scales appropriate for understanding and monitoring changes to the Arctic shelf benthic community; small-scale variation as described here may be overlooked in larger regional studies, but such spatially-focused investigations may be useful going forward as climatic and anthropogenic influences affect the ecosystem.

LITERATURE CITED

Aerts LAM, McFarland AE, Watts BH, Lomac-MacNair KS, Seiser PE, Wisdom SS, Kirk AV, Schudel CA (2013) Marine mammal distribution and abundance in an offshore sub-region of the northeastern Chukchi Sea during the open-water season. Cont Shelf Res, doi: 10.1016/j.csr.2013.04.020

Altabet MA, McCarthy JJ (1985) Temporal and spatial variations in the natural abundance of ^{15}N in PON from a warm-core ring. Deep-Sea Res I 32:755–772

Ambrose Jr WG, von Quillfeldt C, Clough LM, Tilney PVR, Tucker T (2005) The sub-ice algal community in the Chukchi Sea: Large- and small-scale patterns of abundance based on images from a remotely operated vehicle. Polar Biol 28:784–795

Anderson WB, Polis GA (1998) Marine subsidies of island communities in the Gulf of California: Evidence from stable carbon and nitrogen isotopes. Oikos 81:75–80

Antonelis GA, Melin SR, Bukhtiyarov YA (1994) Early spring feeding habits of bearded seals (*Erignathus barbatus*) in the central Bering Sea, 1981. Arctic 47:74–79

Arrington DA, Davidson BK, Winemiller KO, Layman CA (2006) Influence of life history and seasonal hydrology on lipid storage in three neotropical fish species. J Fish Biol 68:1347–1361

Atkinson EG, Wacasey JW (1983) Caloric equivalents for benthic marine organisms from the Canadian Arctic. Can Tech Rep Fish Aquat Sci 1216:vii–31

Bagatini YM, Benedito-Cecilio E, Higuti J (2007) Caloric variability of *Corbicula fluminea* (Mollusca, Bivalvia) in Rosana Reservoir, Brazil. Braz Arch Biol Technol 50:85–90

Bagatini YM, Benedito E, Higuti J (2010) Effect of the environmental factors on the caloric content of benthic and phytophilous invertebrates in neotropical reservoirs in the Paraná State, Brazil. Int Rev Hydrobiol 95:246–259

Ball JR, Esler D, Schmutz JA (2007) Proximate composition, energetic value, and relative abundance of prey fish from the inshore eastern Bering Sea: Implications for piscivorous predators. Polar Biol 30:699–708

Belicka LL, Macdonald RW, Harvey HR (2002) Sources and transport of organic carbon to shelf, slope, and basin surface sediments of the Arctic Ocean. Deep-Sea Res I 49:1463–1483

Ben-David M, Flaherty EA (2012) Stable isotopes in mammalian research: A beginner's guide. J Mammal 93:312–328

Blanchard AL, Parris CL, Knowlton AL, Wade NR (2013a) Benthic ecology of the northeastern Chukchi Sea. Part I. Environmental characteristics and macrofaunal community structure, 2008–2010. Cont Shelf Res, doi: 10.1016/j.csr.2013.04.021

Blanchard AL, Parris CL, Knowlton AL, Wade NR (2013b) Benthic ecology of the northeastern Chukchi Sea. Part II. Spatial variation of megafaunal community structure, 2009–2010. Cont Shelf Res, doi: 10.1016/j.csr.2013.04.031

Bluhm BA, Gradinger R (2008) Regional variability in food availability for arctic marine mammals. Ecol Appl 18:S77–S96

Bluhm BA, Iken K, Mincks-Hardy S, Sirenko BI, Holladay BA (2009) Community structure of epibenthic megafauna in the Chukchi Sea. Aquat Biol 7:269–293

Brawn VM, Peer DL, Bentley RJ (1968) Caloric content of the standing crop of benthic and epibenthic invertebrates of St. Margaret's Bay, Nova Scotia. J Fish Res Board Can 25:1803–1811

Burkhardt S, Riebesell U, Zondervan I (1999) Effects of growth rate, CO_2 concentration, and cell size on the stable carbon isotope fractionation in marine phytoplankton. Geochim Cosmochim Acta 63:3729–3741

Carroll SS, Horstmann-Dehn L, Norcross BL (2013) Diet history of ice seals using stable isotope ratios in claw growth bands. Can J Zool 91:191–202

Checkley Jr DM, Entzeroth L (1985) Elemental and isotopic fractionation of carbon and nitrogen by marine, planktonic copepods and implications to the marine nitrogen cycle. J Plankton Res 7:553–568

Coyle KO, Highsmith R (1994) Benthic amphipod community in the northern Bering Sea: Analysis of potential structuring mechanisms. Mar Ecol Prog Ser 107:233–244

Darling JD, Keogh KE, Steeves TE (1998) Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island, B. C. Mar Mamm Sci 14:692–720

Day RH, Weingartner TJ, Hopcroft RR, Aerts LAM, Blanchard AL, Gall AE,

Gallaway BJ, Hannay DE, Holladay BA, Mathis JT, Norcross BL, Questel JM, Wisdom SS (2013) The offshore northeastern Chukchi Sea: A complex high-latitude ecosystem. Cont Shelf Res, doi: 10.1016/j.csr.2013.02.002

De Leo FC, Smith CR, Rowden AA, Bowden DA, Clark MR (2010) Submarine canyons: Hotspots of benthic biomass and productivity in the deep sea. Proc R Soc Lond, Ser B: Biol Sci 277:2783–2792

Dehn LA, Sheffield GG, Follmann EH, Duffy LK, Thomas DL, O'Hara TM (2007) Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. Polar Biol 30:167–181

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochim Cosmochim Acta 45:341–351

Desrosiers G, Savenkoff C, Olivier M, Stora G, Juniper K, Caron A, Gagné JP, Legendre L, Mulsow S, Grant J, Roy S, Grehan A, Scaps P, Silverberg N, Klein B, Tremblay JÉ, Therriault JC (2000) Trophic structure of macrobenthos in the Gulf of St. Lawrence and on the Scotian Shelf. Deep-Sea Res II 47:663–697

Dorgelo J, Leonards PEG (2001) Relationship between C/N ratio of food types and growth rate in the snail *Potamopyrgus jenkinsi* (E. A. Smith). J N Am Benthol Soc 20:60–67

Dubois S, Orvain F, Marin-Léal JC, Ropert M, Lefebvre S (2007) Small-scale spatial variability of food partitioning between cultivated oysters and associated suspension-feeding species, as revealed by stable isotopes. Mar Ecol Prog Ser 336:151–160

Dunton KH, Saupe SM, Golikov AN, Schell DM, Schonberg SV (1989) Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. Mar Ecol Prog Ser 56:89–97

Dunton KH, Goodall JL, Schonberg SV, Grebmeier JM, Maidment DR (2005) Multi-decadal synthesis of benthic-pelagic coupling in the western arctic: Role of cross-shelf advective processes. Deep-Sea Res II 52:3462–3477

Dunton KH, Schonberg SV, Cooper LW (2012) Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. Estuaries Coasts 35:416–435

Eckman JE, Nowell ARM, Jumars PA (1981) Sediment destabilization by animal tubes. J Mar Res 39:361–374

Emlen JM (1966) The role of time and energy in food preference. Am Nat 100:611–617

Falkowski PG (1991) Species variability in the fractionation of ^{13}C and ^{12}C by marine phytoplankton. J Plankton Res 13:21–28

Fanelli E, Cartes JE, Badalamenti F, Rumolo P, Sprovieri M (2009) Trophodynamics of suprabenthic fauna on coastal muddy bottoms of the southern Tyrrhenian Sea (western Mediterranean). J Sea Res 61:174–187

Fauchald K, Jumars P (1979) The diet of worms: A study of polychaete feeding guilds. Oceanogr Mar Biol Annu Rev 17:193–284

Fay FH (1982) Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. United States Department of Interior Fish and Wildlife Service, North American Fauna 74, Washington, D.C.

Feder HM, Foster NR, Jewett SC, Weingartner TJ, Baxteer R (1994b) Mollusks in the northeastern Chukchi Sea. Arctic 47:145–163

Feder HM, Naidu AS, Jewett SC, Hameedi JM, Johnson WR, Whitledge TE (1994a) The northeastern Chukchi Sea: Benthos-environmental interactions. Mar Ecol Prog Ser 111:171–190

Feder HM, Jewett SC, Blanchard A (2005) Southeastern Chukchi Sea (Alaska) epibenthos. Polar Biol 28:402–421

Feder HM, Jewett SC, Blanchard AL (2007) Southeastern Chukchi Sea (Alaska) macrobenthos. Polar Biol 30:261–275

Feder HM, Iken K, Blanchard AL, Jewett SC, Schonberg S (2011) Benthic food web structure in the southeastern Chukchi Sea: An assessment using $\delta^{13}C$ and $\delta^{15}N$ analyses. Polar Biol 34:521–532

Fisher K, Stewart R, Kastelein R, Campbell L (1992) Apparent digestive efficiency in walruses (*Odobenus rosmarus*) fed herring (*Clupea harengus*) and clams (*Spisula* sp.). Can J Zool 70:30–36

Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for the isolation and purification of total lipids from animal tissues. J Biol Chem 226:497–509

Freudenthal T, Wagner T, Wenzhöfer F, Zabel M, Wefer G (2001) Early diagenesis of organic matter from sediments of the eastern subtropical Atlantic: Evidence from stable nitrogen and carbon isotopes. Geochim Cosmochim Acta 65:1795–1808

Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnol Oceanogr 33:1182–1190

Fry B, Wainright SC (1991) Diatom sources of super ^{13}C-rich carbon in marine food webs. Mar Ecol Prog Ser 76:149–157

Gall AE, Day RH, Weingartner TJ (2013) Structure and variability of the marine-bird community in the northeastern Chukchi Sea. Cont Shelf Res, doi: 10.1016/j.csr.2012.11.004

Gilbert JR (1989) Aerial census of Pacific walruses in the Chukchi Sea, 1985. Mar Mamm Sci 5:17–28

Glud RN, Woelfel J, Karsten U, Kühl M, Rysgaard S (2009) Benthic microalgal production in the Arctic: Applied methods and status of the current database. Bot Mar 52:559–571

Gnaiger E, Bitterlich G (1984) Proximate biochemical composition and caloric content calculated from elemental CHN analysis: A stoichiometric concept. Oecologia 62:289–298

Gradinger R (2009) Sea-ice algae: Major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. Deep-Sea Res II 56:1201–1212

Granger J, Prokopenko MG, Sigman DM, Mordy CW, Morse ZM, Morales LV, Sambrotto RN, Plessen B (2011) Coupled nitrification-denitrification in sediment of the eastern Bering Sea shelf leads to ^{15}N enrichment of fixed N in shelf waters. J Geophys Res (C Oceans) 116:C11006

Grebmeier JM (1993) Studies of pelagic-benthic coupling extended onto the Soviet continental shelf in the northern Bering and Chukchi seas. Cont Shelf Res 13:653–668

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and Sub-Arctic Seas. Annu Rev Mar Sci 4:63–78

Grebmeier JM, Barry JP (1991) The influence of oceanographic processes on pelagic-benthic coupling in polar regions: A benthic perspective. J Mar Syst 2:495–518

Grebmeier JM, McRoy CP (1989) Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. Mar Ecol Prog Ser 53:93–100

Grebmeier JM, Feder HM, McRoy CP (1989) Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. II. Benthic community structure. Mar Ecol Prog Ser 51:253–268

Grebmeier JM, McRoy CP, Feder HM (1988) Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi seas. I. Food supply source and benthic biomass. Mar Ecol Prog Ser 48:57–67

Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006) Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. Prog Oceanogr 71:331–361

Haecky P, Jonsson S, Andersson A (1998) Influence of sea ice on the composition of the spring phytoplankton bloom in the northern Baltic Sea. Polar Biol 20:1–8

Herman PMJ, Middelburg JJ, Widdows J, Lucas CHR, Heip CH (2000) Stable isotopes as trophic tracers: Combining field sampling and manipulative labelling of food resources for macrobenthos. Mar Ecol Prog Ser 204:79–92

Hill V, Cota G (2005) Spatial patterns of primary production in the Chukchi Sea in the spring and summer of 2002. Deep-Sea Res II 52:3344–3354

Hill V, Cota G, Stockwell D (2005) Spring and summer phytoplankton communities in the Chukchi and Eastern Beaufort Seas. Deep-Sea Res II 52:3369–3385

Hobson KA, Ambrose Jr WG, Renaud PE (1995) Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: Insights from $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar Ecol Prog Ser 128:1–10

Hobson KA, Fisk A, Karnovsky N, Holst M, Gagnon JM, Fortier M (2002) A stable isotope ($\delta^{13}C$, $\delta^{15}N$) model for the North Water food web: Implications for evaluating trophodynamics and the flow of energy and contaminants. Deep-Sea Res II 49:5131–5150

Holte B, Gulliksen B (1998) Common macrofaunal dominant species in the sediments of some north Norwegian and Svalbard glacial fjords. Polar Biol 19:375–382

Hondolero D, Bluhm BA, Iken K (2012) Caloric content of dominant benthic species from the northern Bering and Chukchi Seas: Historical comparisons and the effects of preservation. Polar Biol 35:637–644

Iken K, Bluhm BA, Gradinger R (2005) Food web structure in the high Arctic Canada Basin: Evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. Polar Biol 28:238–249

Iken K, Bluhm B, Dunton K (2010) Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep-Sea Res II 57:71–85

Jorde DG, Owen RB (1990) Changes in caloric content of the amphipod *Gammarus oceanicus* along the coast of Maine. Can Field-Nat 104:303–304

Jay CV, Fischbach AS, Kochnev AA (2012) Walrus areas of use in the Chukchi Sea during sparse sea ice cover. Mar Ecol Prog Ser 468:1–13

Kang CK, Kim JB, Lee KS, Kim JB, Lee PY, Hong JS (2003) Trophic importance of benthic microalgae to macrozoobenthos in coastal bay systems in Korea: Dual stable C and N isotope analyses. Mar Ecol Prog Ser 259:79–92

Kaufman MR, Gradinger RR, Bluhm BA, O'Brien DM (2008) Using stable isotopes to assess carbon and nitrogen turnover in the Arctic sympagic amphipod *Onisimus litoralis*. Oecologia 158:11–22

Kędra M, Murina G (2007) The sipunculan fauna of Svalbard. Polar Res 26:37–47

Kędra M, Kuliński K, Walkusz W, Legeżyńska J (2012) The shallow benthic food web structure in the high Arctic does not follow seasonal changes in the surrounding environment. Estuar Coast Shelf Sci 114:183–191

Kopczyńska EE, Goeyens L, Semeneh M, Dehairs F (1995) Phytoplankton composition and cell carbon distribution in Prydz Bay, Antarctica: Relation to organic particulate matter and its $\delta^{13}C$ values. J Plankton Res 17:685–707

Korb RE, Raven JA, Johnston AM, Leftley JW (1996) Effects of cell size and specific growth rate on stable carbon isotope discrimination by two species of marine diatom. Mar Ecol Prog Ser 143:283–288

Lavoie D, Macdonald RW, Denman KL (2009) Primary productivity and export fluxes on the Canadian shelf of the Beaufort Sea: A modelling study. J Mar Syst 75:17–32

Laws EA, Archie JW (1981) Appropriate use of regression analysis in marine biology. Mar Biol 65:13–16

Lawson JW, Magalhaes AM, Miller EH (1998) Important prey species of marine vertebrate predators in the northwest Atlantic: Proximate composition and energy density. Mar Ecol Prog Ser 164:13–20

Leu E, Wiktor J, Søreide JE, Berge J, Falk-Petersen S (2010) Increased irradiance reduces food quality of sea ice algae. Mar Ecol Prog Ser 411:49–60

Levin L, Blair N, DeMaster D, Plaia G, Fornes W, Martin C, Thomas C (1997) Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. J Mar Res 55:595–611

Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lutcavage ME (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: Comparison of chemical extraction and modelling methods. J Anim Ecol 77:838–846

Lowry LF, Frost KJ, Burns JJ (1980) Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walruses. Arctic 33:330–342

Martin S, Drucker R (1997) The effect of possible Taylor columns on the summer ice retreat in the Chukchi Sea. J Geophys Res 102:10473–10482

Matheke GEM, Horner R (1974) Primary productivity of the benthic microalgae in the Chukchi Sea near Barrow, Alaska. J Fish Res Board Can 31:1779–1786

McClelland JW, Valiela I, Michener RH (1997) Nitrogen-stable isotope signatures in estuarine food webs: A record of increasing urbanization in coastal watersheds. Limnol Oceanogr 42:930–937

McMahon KW, Ambrose Jr WG, Johnson BJ, Sun MY, Lopez GR, Clough LM, Carroll ML (2006) Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. Mar Ecol Prog Ser 310:1–14

McMinn A, Hirawake T, Hamaoka T, Hattori H, Fukuchi M (2005) Contribution of benthic microalgae to ice covered coastal ecosystems in northern Hokkaido, Japan. J Mar Biol Assoc UK 85:283–289

McTigue ND, Schonberg, SV, Dunton KH (2012) Trophodynamics of the northeastern Chukchi Sea food webs based on stable ^{13}C and ^{15}N isotopic ratios. In: Dunton KH (ed) Chukchi Sea Offshore Monitoring in Drilling Area (COMIDA): Chemical and Benthos (CAB) Final Report to Bureau of Ocean Energy Management, p 196–232

Michel C, Legendre L, Therriault JC, Demers S, Vandevelde T (1993) Springtime coupling between ice algal and phytoplankton assemblages in southeastern Hudson Bay, Canadian Arctic. Polar Biol 13:441–449

Michener RH, Kaufman L (2007) Stable isotope ratios as tracers in marine food webs: an update. In: Michener R, Lajtha K (eds) Stable Isotopes in Ecology and Environmental Sciences. Blackwell Publishing, Malden, MA, p 238–282

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochim Cosmochim Acta 48:1135–1140

Mincks SL, Smith CR, Jeffreys RM, Sumida PYG (2008) Trophic structure on the West Antarctic Peninsula shelf: Detritivory and benthic inertia revealed by $\delta^{13}C$ and $\delta^{15}N$ analysis. Deep-Sea Res II 55:2502–2514

Mysak LA, Manak DK (1989) Arctic sea-ice extent and anomalies, 1953–1984. Atmosphere-Ocean 27:376–405

Naidu AS, Scalan RS, Feder HM, Goering JJ, Hameedi MJ, Parker PL, Behrens EW, Caughey ME, Jewett SC (1993) Stable organic carbon isotopes in sediments of the north Bering-south Chukchi seas, Alaskan-Soviet Arctic Shelf. Cont Shelf Res 13:669–691

Naidu AS, Cooper LW, Finney BP, Macdonald RW, Alexander C, Semiletov IP (2000) Organic carbon isotope ratios ($\delta^{13}C$) of Arctic Amerasian continental shelf sediments. Int J Earth Sci 89:522–532

Österblom H, Olsson O, Blenckner T, Furness RW (2008) Junk-food in marine ecosystems. Oikos 117:967–977

Oug E (2000) Soft-bottom macrofauna in the high-latitude ecosystem of Balsfjord, northern Norway: Species composition, community structure and temporal variability. Sarsia 85:1–13

Parsons TR, Maita Y, Lalli CM (1984) A manual for chemical and biological methods in seawater analysis. Pergamon Press, Toronto, Canada

Parsons TR, Takahashi, M, Hargrave, B (1984) Biological Oceanographic Processes. Pergamon Press, New York, NY

Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. ICES J Mar Sci 55:467–481

Perry G, Pianka ER (1997) Animal foraging: Past, present and future. Trends Ecol Evol 12:360–364

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

Piepenburg D (2005) Recent research on Arctic benthos: Common notions need to be revised. Polar Biol 28:733–755

Post DM (2002) Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83:703–718

Post JR, Parkinson EA (2001) Energy allocation strategy in young fish: Allometry and survival. Ecology 82:1040–1051

Quakenbush L, Citta J, Crawford J (2011a) Biology of the Bearded Seal (*Erignathus barbatus*) in Alaska, 1961–2009. Final Report to National Marine Fisheries Service. Alaska Department of Fish and Game, Fairbanks, AK

Quakenbush L, Citta J, Crawford J (2011b) Biology of the Ringed Seal (*Phoca hispida*) in Alaska, 1960–2010. Final Report to National Marine Fisheries Service. Alaska Department of Fish and Game, Fairbanks, AK

Questel JM, Clarke C, Hopcroft RR (2013) Seasonal and interannual variation in the planktonic communities of the northeastern Chukchi Sea during the summer and early fall. Cont Shelf Res, doi: 10.1016/j.csr.2012.11.003

Quinn GP, Keough MJ (2002) Correlation and regression. In: Experimental Design and Data Analysis for Biologists. Cambridge University Press, New York, NY, p 72–110

Raffaelli D (2000) Trends in research on shallow water food webs. J Exp Mar Biol Ecol 250:223–232

Ray GC, McCormick-Ray J, Berg P, Epstein HE (2006) Pacific walrus: Benthic bioturbator of Beringia. J Exp Mar Biol Ecol 330:403–419

Rhoads DC, Young DK (1970) The influence of deposit-feeding organisms on sediment stability and community trophic structure. J Mar Res 28:150–178

Rice RL, McCumby KI, Feder HM (1980) Food of *Pandalus borealis*, *Pandalus hypsinotus* and *Pandalus goniurus* (Pandalidae, Decapoda) from Lower Cook Inlet, Alaska. Proc Natl Shellfish Ass 70:47–54

Rosen DAS, Trites AW (2000) Pollock and the decline of Steller sea lions: Testing the junk-food hypothesis. Can J Zool 78:1243–1250

Rosen DAS, Trites AW (2004) Satiation and compensation for short-term changes in food quality and availability in young Steller sea lions (*Eumetopias jubatus*). Can J Zool 82:1061–1069

Rosen DAS, Winship AJ, Hoopes LA (2007) Thermal and digestive constraints to foraging behaviour in marine mammals. Philos Trans R Soc Lond, Ser B: Biol Sci 362:2151–2168

Rosenberg R (1995) Benthic marine fauna structured by hydrodynamic processes and food availability. Netherlands J Sea Res 34:303–317

Sakshaug E (2004) Primary and secondary production in the Arctic seas. In: Stein R, Macdonald, RW (eds) The Organic Carbon Cycle in the Arctic Ocean. Springer, New York, NY, p 57–81

Saupe SM, Schell DM, Griffiths WB (1989) Carbon-isotope ratio gradients in western arctic zooplankton. Mar Biol 103:427–432

Sheffield G, Fay FH, Feder H, Kelly BP (2001) Laboratory digestion of prey and interpretation of walrus stomach contents. Mar Mamm Sci 17:310–330

Sheffield G, Grebmeier JM (2009) Pacific walrus (*Odobenus rosmarus divergens*): differential prey digestion and diet. Mar Mamm Sci 25:761–777

Snelgrove PVR, Butman CA (1994) Animal-sediment relationships revisited: Cause versus effect. Oceanogr Mar Biol Ann Rev 32:111–177

Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Prog Oceanogr 71:59–87

Sotiropoulos MA, Tonn WM, Wassenaar LI (2004) Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: Potential consequences for food web studies. Ecol Freshw Fish 13:155–160

Spall MA (2007) Circulation and water mass transformation in a model of the Chukchi Sea. J Geophys Res 112:C05025

Speckman SG, Chernook VI, Burn DM, Udevitz MS, Kochnev AA, Vasilev A, Jay CV, Lisovsky A, Fischbach AS, Benter RB (2011) Results and evaluation of a survey to estimate Pacific walrus population size, 2006. Mar Mamm Sci 27:514–553

Spitz J, Trites AW, Becquet V, Brind'Amour A, Cherel Y, Galois R, Ridoux V (2012) Cost of living dictates what whales, dolphins and porpoises eat: The importance of prey quality on predator foraging strategies. PLoS ONE 7:e50096

Sun MY, Carroll ML, Ambrose Jr WG, Clough LM, Zou L, Lopez GR (2007) Rapid consumption of phytoplankton and ice algae by Arctic soft-sediment benthic communities: Evidence using natural and ^{13}C-labeled food materials. J Mar Res 65:561–588

Syvertsen EE (1991) Ice algae in the Barents Sea: Types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom. Polar Res 10:277–288

Tamelander T, Kivimäe C, Bellerby RGJ, Renaud PE, Kristiansen S (2009) Base-line variations in stable isotope values in an Arctic marine ecosystem: Effects of carbon and nitrogen uptake by phytoplankton. Hydrobiologia 630:63–73

Taylor JD (1978) The diet of *Buccinum undatum* and *Neptunea antiqua* (Gastropoda: Buccinidae). J Conchol 29:309–318

Taylor BR, Roff JC (1984) Use of ATP and carbon: nitrogen ratio as indicators of food quality of stream detritus. Freshw Biol 14:195–201

Tremblay JÉ, Michel C, Hobson KA, Gosselin M, Price NM (2006) Bloom dynamics in early opening waters of the Arctic Ocean. Limnol Oceanogr 51:900–912

Trites AW, Donnelly CP (2003) The decline of Steller sea lions *Eumetopias jubatus* in Alaska: A review of the nutritional stress hypothesis. Mamm Rev 33:3–28

Valiela I (1995) Marine Ecological Processes. Springer, New York, NY

Vander Zanden M, Rasmussen JB (2001) Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. Limnol Oceanogr 46:2061–2066

Young DK, Rhoads DC (1971) Animal-sediment relations in Cape Cod Bay, Massachusetts I. A transect study. Mar Biol 11:242–254

Wacasey JW, Atkinson EG (1987) Energy values of marine benthic invertebrates from the Canadian Arctic. Mar Ecol Prog Ser 39:243–250

Walsh JJ (1980) Shelf-sea ecosystems. In: Longhurst AR (ed) Analysis of Marine Ecosystems. Academic Press, New York, NY, p 159–189

Walsh JJ, McRoy CP (1986) Ecosystem analysis in the southeastern Bering Sea. Cont Shelf Res 5:259–288

Wang J, Cota GF, Comiso JC (2005) Phytoplankton in the Beaufort and Chukchi Seas: Distribution, dynamics, and environmental forcing. Deep-Sea Res II 52:3355–3368

Weems J, Iken K, Gradinger R, Wooller MJ (2012) Carbon and nitrogen assimilation in the Bering Sea clams *Nuculana radiata* and *Macoma moesta*. J Exp Mar Biol Ecol 430:32–42

Weingartner TJ, Cavalieri DJ, Aagaard K, Sasaki Y (1998) Circulation, dense water formation, and outflow on the northeast Chukchi shelf. J Geophys Res 103:7647–7661

Weingartner T, Aagaard K, Woodgate R, Danielson S, Sasaki Y, Cavalieri D (2005) Circulation on the north central Chukchi Sea shelf. Deep-Sea Res II 52:3150–3174

Weingartner T, Dobbins E, Danielson S, Winsor P, Potter R, Statscewich H (2013) Hydrographic variability over the northeastern Chukchi Sea shelf in summer-fall 2008–2010. Cont Shelf Res, doi: 10.1016/j.csr.2013.03.012

Wesławski JM, Kwaśniewski S, Stempniewicz L, Błachowiak-Samołyk K (2006) Biodiversity and energy transfer to top trophic levels in two contrasting Arctic fjords. Pol Polar Res 27:259–278

Winsor P, Chapman DC (2004) Pathways of Pacific water across the Chukchi Sea: a numerical model study. J Geophys Res 109:C03002

Woodgate RA, Aagaard K, Weingartner TJ (2005) A year in the physical oceanography of the Chukchi Sea: Moored measurements from autumn 1990–1991. Deep-Sea Res II 52:3116–3149

Woodgate RA, Weingartner T, Lindsay R (2010) The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. Geophys Res Lett 37:L01602

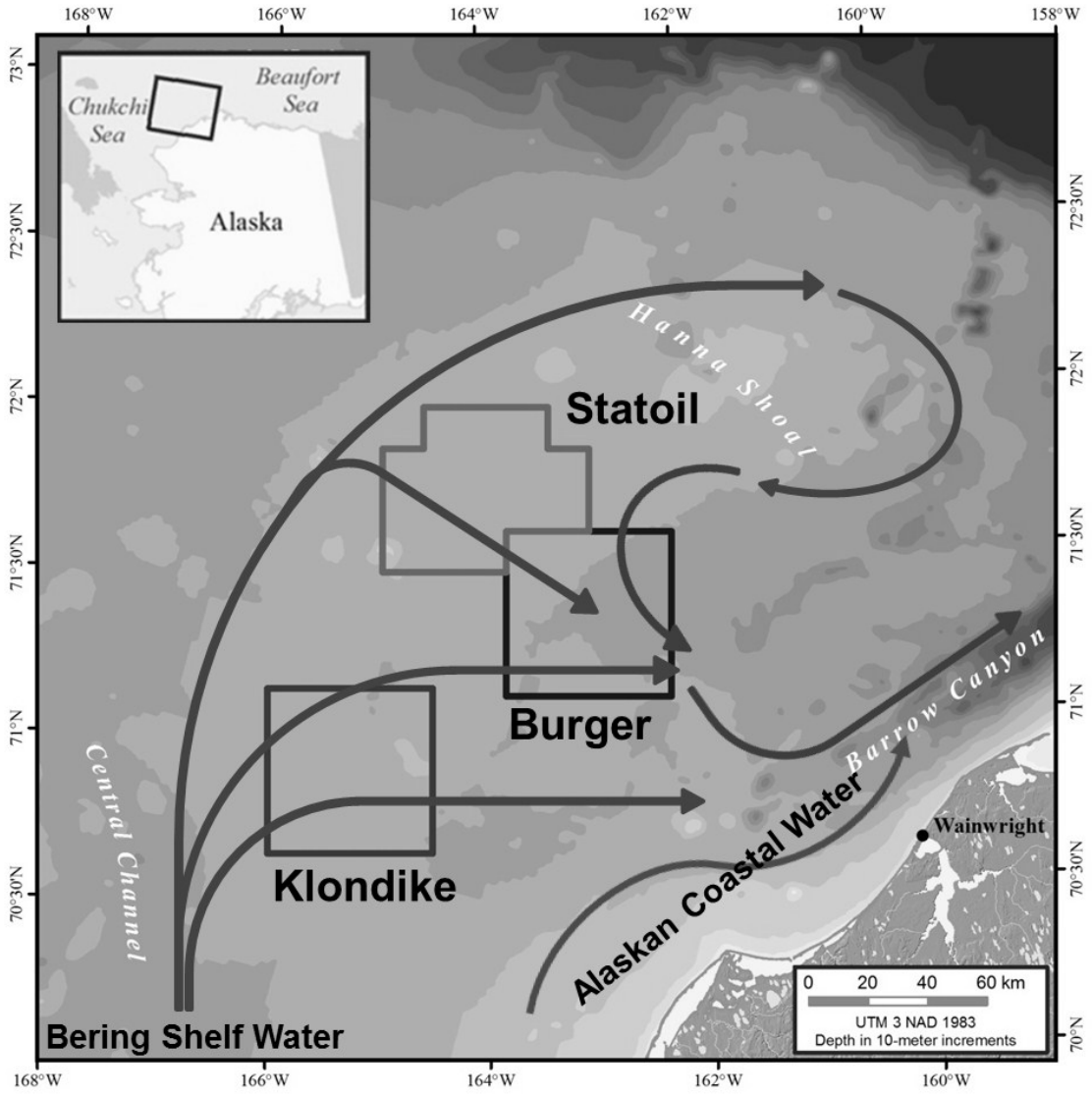

Figure 1. Map of the overall study region. The three study areas (Klondike, Burger, and Statoil) are denoted in boxes. Conceptual oceanographic circulation (indicated by arrows) based on Winsor & Chapman (2004), Spall (2007), and Weingartner et al. (2013).

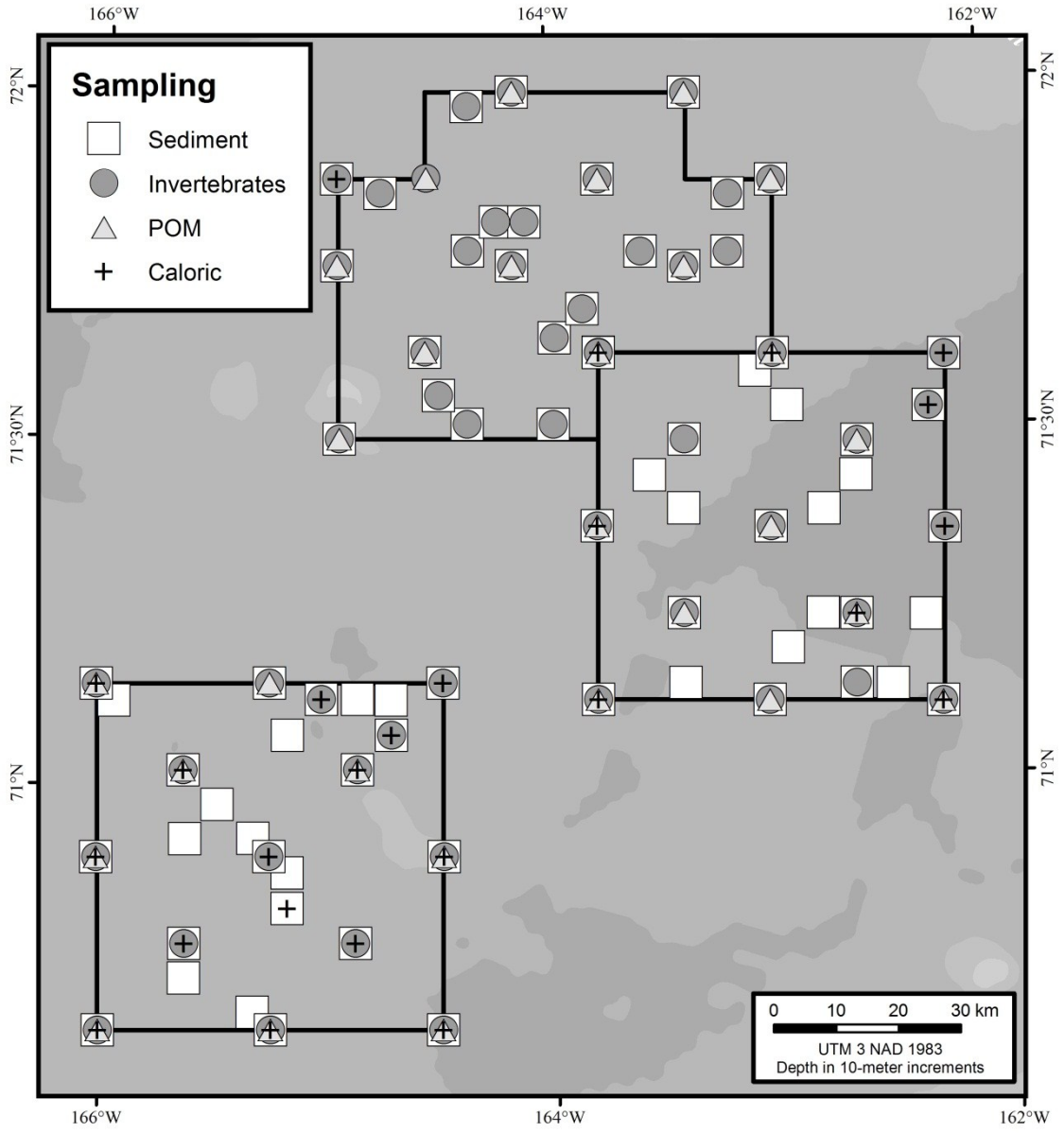

Figure 2. Map of samples taken at stations within the Klondike, Burger, and Statoil study areas. The three sample types for stable carbon and nitrogen isotope analysis (sediments, invertebrates, POM) are indicated by squares, circles, and triangles, respectively. Caloric samples (invertebrates) are indicated by crosses.

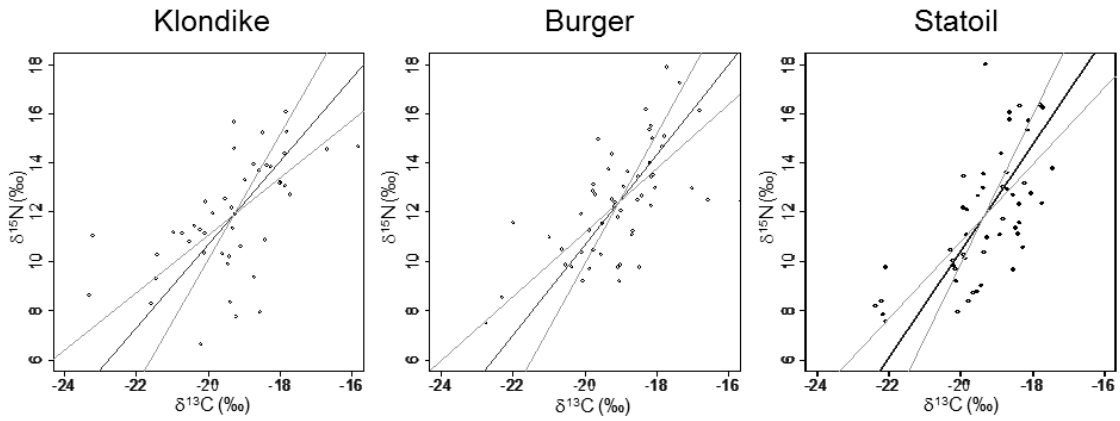

Figure 3. Ranged major axis (RMA) regression of benthic invertebrate stable carbon and nitrogen isotope data from Klondike, Burger, and Statoil. Each point represents the mean stable carbon and nitrogen isotope signature of one taxon. The center line is the fitted linear model, with slope 95% confidence intervals denoted above and below the fitted line.

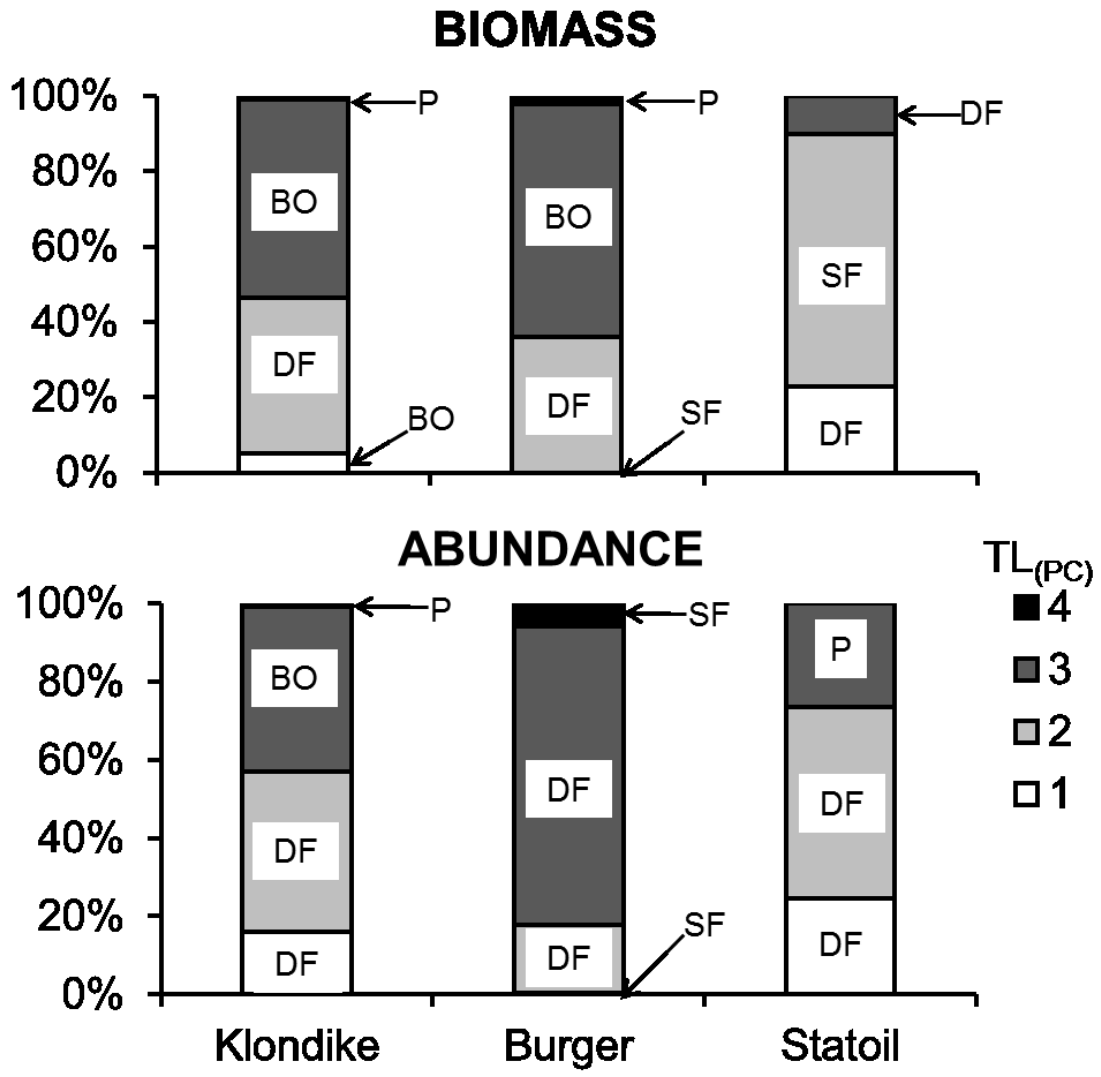

Figure 4. Proportional contributions of benthic biomass and abundance of taxa to each trophic level at Klondike, Burger, and Statoil. Trophic level is based on the primary consumer *Ampelisca eschrichti* ($TL_{(PC)}$=2, see Methods section for details). The feeding mode of the taxa with the highest biomass/abundance contributing to each trophic level is noted within each bar. Feeding modes: BO benthic omnivore, DF deposit feeder (includes surface and subsurface), SF suspension feeder, P predator.

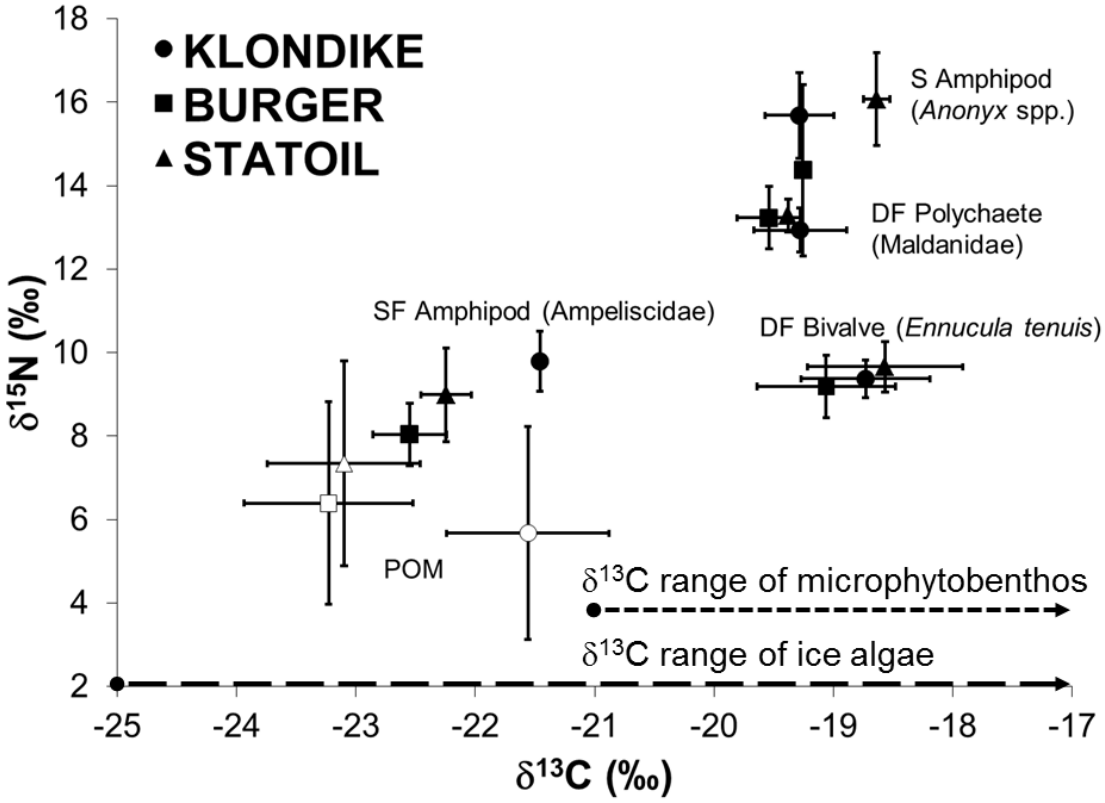

Figure 5. Stable nitrogen vs. carbon isotope ratios of four benthic invertebrate taxa (closed symbols) and POM (open symbols) at Klondike, Burger, and Statoil. Each point represents a mean with standard deviation (SD) bars. Feeding modes: DF: Deposit feeder (includes surface and subsurface), S: Scavenger, SF: Suspension feeder. Ice algal and microphytobenthos $\delta^{13}C$ range values from France (1995), Tremblay et al. (2006), and Gradinger (2009) for comparison of organism stable isotope ratios with those of potential food sources (see Discussion).

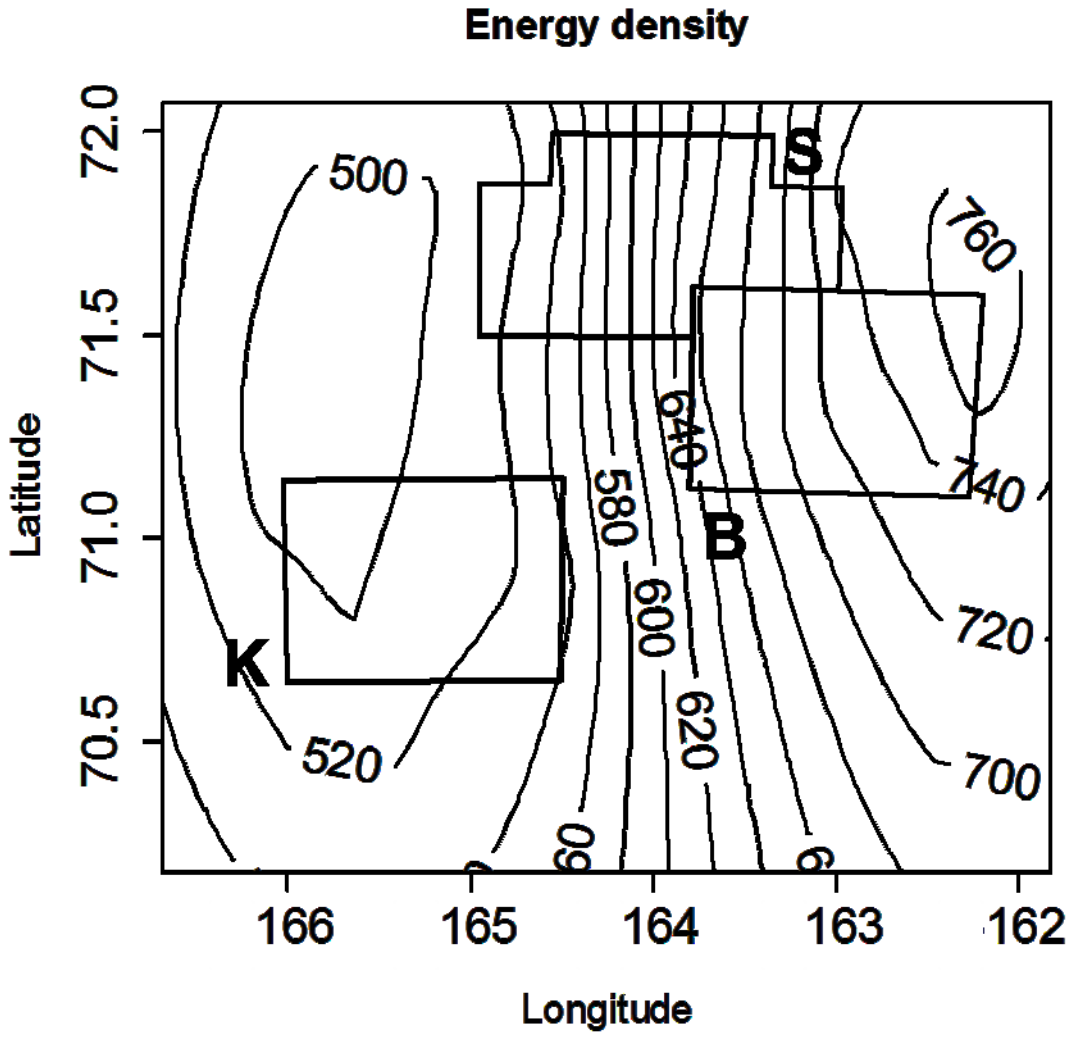

Figure 6. Spatial model of potential prey gross energy density in kJ WM m^{-2}. Study areas are indicated by the first letter of their name: B: Burger, K: Klondike, S: Statoil.

Table 1. Mean and standard deviation (SD) of 2009–2011 biomass (g WM m^{-2}) and abundance (individuals m^{-2}) data for the macro- and megafaunal community at Klondike, Burger, and Statoil. Values are based on biomass and abundance data from Blanchard et al. (2013a, b).

	Klondike	
	Mean	SD
Biomass (g WM m^{-2})	154.67	38.32
Abundance (individuals m^{-2})	1355.33	592.41
	Burger	
	Mean	SD
Biomass (g WM m^{-2})	310.10	59.92
Abundance (individuals m^{-2})	3695.03	1133.03
	Statoil	
	Mean	SD
Biomass (g WM m^{-2})	307.50	65.47
Abundance (individuals m^{-2})	1205.00	219.20

Table 2. P-values for one-way ANOVA with Tukey multiple comparisons of sediment and POM stable carbon and nitrogen isotope data and C/N ratios, as well as two-way ANOVA of interannual sediment isotope data. Values significant at $\alpha = 0.05$ are in bold.

	POM			**SEDIMENT**		
	$\delta^{13}C$	$\delta^{15}N$	C/N	$\delta^{13}C$	$\delta^{15}N$	C/N
ANOVA	**<0.001**	0.332	0.150	**<0.001**	**0.002**	**<0.001**
Klondike - Burger	**<0.001**	0.802	0.127	0.073	**0.001**	**0.019**
Burger - Statoil	0.891	0.659	0.612	0.078	0.344	0.143
Klondike - Statoil	**<0.001**	0.306	0.499	**<0.001**	0.070	**<0.001**
Year	-	-	-	0.469	0.978	0.226
Study Area	-	-	-	**0.034**	**<0.001**	**0.040**
Year*Study Area	-	-	-	0.524	0.847	0.196

Table 3. Stable carbon and nitrogen isotope data of POM, sediments, and benthic invertebrates collected from Klondike, Burger, and Statoil. Values are reported as means with standard deviation (SD), number of replicates (n), trophic level (TL) based on a primary consumer (see Methods for details), and feeding type (BO benthic omnivore, DF deposit feeder [includes surface and subsurface], GR grazer, P predator, S scavenger, SF suspension feeder).

Species/Taxon	Feeding type	Klondike						Burger						Statoil					
		$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL	$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL	$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL
POM		-21.56	0.68	5.67	2.55	9		-23.23	0.71	6.39	2.43	10		-23.10	0.64	7.34	2.45	11	
Sediment		-22.75	0.39	4.99	1.04	26		-22.51	0.40	5.97	0.84	26		-22.28	0.32	5.60	0.95	24	
CNIDARIA																			
Actinaria																			
Gersemia rubiformis	P							-18.12		13.51		1	3.5						
Stomphia spp.	P	-19.30		14.60		1	3.6												
Hydrozoa	SF							-20.10		10.39		1	2.5	-19.38	1.16	10.40	1.01	5	2.2
NEMERTEA	P							-17.39		17.27		1	4.6						
SIPUNCULA	DF																		
Sipunculid	DF	-18.44		10.89		1	2.5												
Golfingia spp.	DF													-20.16		9.71		1	2.0
Golfingia margaritacea	DF	-19.34	0.52	11.38	0.05	2	2.6	-18.68		11.27		1	2.8	-19.28		10.99		1	2.4
Phascolion strombus	DF							-18.82	0.84	13.66	0.40	2	3.5	-19.84		12.12		1	2.7
PRIAPULA																			
Priapulus caudatus	DF	-17.88		14.41		1	3.5	-18.18	0.28	15.52	0.11	2	4.0	-18.10	0.42	15.71	0.45	3	3.7
POLYCHAETA																			
Ampharetidae	DF	-20.76		11.16		1	2.6	-21.01		10.99		1	2.7	-18.73		12.95		1	2.9
Axiothella catenata	DF	-19.37		12.22		1	2.9							-18.83		13.06		1	3.0
Axiothella spp.	DF	-18.77	0.35	13.98	0.14	2	3.4												
Brada spp.	DF							-19.19		12.25		1	3.1						
Capitellidae	DF							-18.42		12.68		1	3.2	-18.83		11.74		1	2.6
Cirratulidae	DF													-20.21		9.83		1	2.0
Flabelligeridae	DF	-23.34		8.61		1	1.8												

Table 3. (*continued*)

Species/Taxon	Feeding type	Klondike						Burger						Statoil					
		$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL	$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL	$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL
Idanthyrsus spp.	SF	-20.11		11.17		1	2.6												
Lumbrineris spp.	P							-18.54	0.21	13.45	1.54	3	3.4	-18.72	0.75	13.64	0.54	3	3.1
Maldane sarsi	DF	-19.00	0.48	13.31	0.58	13	3.2	-19.35	0.70	13.75	0.95	6	3.5	-19.36	0.61	13.55	1.13	16	3.1
Maldanidae	DF	-19.56	1.00	12.56	1.99	15	3.0	-19.73	0.45	12.70	1.42	19	3.2	-19.39	0.38	13.00	1.11	31	2.9
Nephtys spp.	P	-17.85		16.11		1	4.0	-17.74		17.91		1	4.8	-18.15	0.57	15.36	0.49	6	3.6
Ophelina spp.	DF	-19.90	0.31	11.98	0.24	2	2.8												
Paradiopatra parva	P	-18.38		13.94		1	3.4							-18.36	0.66	11.57	0.66	6	2.5
Phyllodocidae	P							-18.32	0.12	16.21	0.11	2	4.3	-17.79		16.37		1	3.9
Polynoidae	P	-18.27		13.85		1	3.3	-19.00	0.40	12.08	1.00	2	3.0	-19.52	0.55	12.70	1.09	5	2.9
Praxillella praetermissa	DF	-17.87		13.08		1	3.1												
Praxillella spp.	DF													-18.24		13.19		1	3.0
Sabellidae	SF	-20.98		11.20		1	2.6												
Sternaspis fossor	DF	-19.48		9.92		1	2.2							-18.39	0.72	12.34	1.84	3	2.8
Terebellidae	DF	-20.12	0.69	12.46	0.66	2	2.9	-19.17		12.42		1	3.1	-19.95		12.21		1	2.7
Terebellides stroemi	DF													-19.86	1.50	11.09	0.90	5	2.4
MOLLUSCA																			
Polyplacophora	GR	-17.82		15.27		1	3.8												
Ishnochiton albus	GR	-16.71		14.57		1	3.6												
Gastropoda																			
Boreotrophon spp.	P							-18.18		12.27		1	3.1						
Buccinum polare	P													-17.71		16.27		1	3.9
Buccinum scalariforme	P							-18.14		15.00		1	3.9						
Buccinum spp.	P													-18.37		16.34		1	3.9
Colus spp.	P	-15.24		17.13		1	4.3	-16.83	0.99	16.16	0.28	2	4.2						
Cryptonatica affinis	P							-18.21		14.02		1	3.6	-18.04		12.78		1	2.9
Cylichna alba	P							-18.18		13.46		1	3.4	-18.88	0.03	14.42	0.51	2	3.4
Euspira pallida	P							-18.05		13.03		1	3.3	-18.57	0.97	12.72	1.21	5	2.9
Margarites spp.	P	-18.60		13.68		1	3.3	-18.70		11.10		1	2.7						

Table 3. (*continued*)

Species/Taxon	Feeding type	Klondike						Burger						Statoil					
		$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL	$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL	$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL
Plicifusus spp.	P																		
Solariella spp.	P	-18.02		13.20		1	3.2	-19.10		11.81		1	3.0						
Tachyrhynchus reticulatus	P													-18.48		11.35		1	2.5
Tachyrhynchus spp.	P	-19.61		10.32		1	2.3												
Bivalvia																			
Astarte borealis	SF							-20.13		11.93		1	3.0	-19.90		10.15		1	2.1
Astarte montagui	SF	-20.40		11.48		1	2.6	-19.54		11.56		1	2.9						
Astarte spp.	SF							-19.10	0.01	9.77	0.02	2	2.4	-18.93	0.72	11.10	0.15	3	2.4
Cyclocardia crebricostata	SF							-20.66		10.48		1	2.6	-18.28		10.57		1	2.2
Ennucula tenuis	DF	-18.73	0.54	9.37	0.45	24	2.0	-19.06	0.48	9.19	0.58	34	2.2	-18.57	0.65	9.66	0.60	73	2.0
Liocyma fluctuosa	SF							-20.55	0.33	9.87	1.21	2	2.4						
Macoma calcarea	DF													-19.79	0.04	8.39	0.32	2	1.6
Macoma moesta	DF													-20.14		9.21		1	1.8
Macoma spp.	DF	-19.41		8.37		1	1.7	-19.89	0.42	9.71	0.45	2	2.3	-19.57	0.26	8.79	0.88	4	1.7
Musculus niger	SF							-18.49		9.76		1	2.4						
Mysella planata	DF							-20.07		9.23		1	2.2						
Nuculana pernula	DF													-19.92		10.27		1	2.1
Nuculana radiata	DF	-19.43		10.21		1	2.3												
Nuculana spp.	DF	-18.57		7.95		1	1.6	-19.77	0.01	10.49	0.02	2	2.6	-20.22		10.05		1	2.1
Serripes groenlandicus	SF/DF													-20.30		10.48		1	2.2
Thyasira flexuosa	DF							-19.79		12.89		1	3.3						
Yoldia spp.	DF													-19.67	0.27	8.73	0.69	5	1.7
Yoldia hyperborea	DF							-19.03		9.88		1	2.4	-19.44		9.02		1	1.8
CHELICERATA																			
Pycnogonidae	P	-20.24		11.30		1	2.6	-18.93		13.06		1	3.3						
CRUSTACEA																			
Amphipoda		-19.24		7.73		1	1.5												
Ampelisca eschrichti	SF	-21.48	0.34	9.29	1.17	2	2.0	-22.33		8.56		1	2.0	-22.10	0.27	9.78	1.00	3	2.0
Ampelisca spp.	SF	-21.44		10.29		1	2.3	-22.77		7.51		1	1.7	-22.39	1.44	8.20	0.94	3	1.5

Table 3. (*continued*)

Species/Taxon	Feeding type	Klondike						Burger						Statoil					
		$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL	$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL	$\delta^{13}C$	SD	$\delta^{15}N$	SD	n	TL
Anonyx spp.	S	-19.29	0.29	15.68	1.03	2	3.9	-19.26	0.02	14.37	2.05	2	3.7	-18.64	0.11	16.07	1.11	4	3.9
Byblis spp.	SF													-22.24	0.65	8.37	1.00	3	1.6
Haploops laevis	SF	-21.63	0.05	8.28	0.66	2	1.7							-22.17	0.52	7.86	0.65	5	1.4
Paraphoxus spp.	SF							-18.22		15.39		1	4.0						
Stegocephalus spp.	S	-19.26		11.93		1	2.8	-19.27		12.54		1	3.2						
Decapoda																			
Chionoecetes opilio	BO	-20.21		6.63		1	1.2	-19.57	0.08	10.29	4.11	2	2.5						
Hippolytidae	BO	-18.51		15.24		1	3.8												
Labidochirus splendescens	BO	-19.11	0.35	10.61	3.01	2	2.4												
Leucon nasica	DF													-20.08	0.35	7.94	1.84	2	1.5
Ostracoda	P							-19.63		14.97		1	3.9	-19.93	0.28	13.51	0.95	3	3.1
Other crustaceans																			
Synidotea spp.	P							-20.37		9.77		1	2.4						
ECHINODERMATA																			
Asteroidea																			
Ctenodiscus crispatus	DF	-17.74		12.72		1	3.0												
Leptasterias groenlandica	P							-16.59	0.40	12.51	0.24	2	3.2						
Leptasterias spp.	P							-15.66		12.47		1	3.2						
Pteraster obscurus	P	-18.01		13.25		1	3.2												
Ophiuroidea																			
Diamphiodia craterodmeta	DF							-18.54		12.52		1	3.2						
Ophiura sarsii	BO	-15.83		14.66		1	3.6	-17.03		12.97		1	3.3	-17.46	0.34	13.79	0.90	2	3.2
Ophiura spp.	BO													-17.73	1.25	12.37	0.64	2	2.8
Ophiuridae	BO							-17.80		15.13		1	3.9	-18.41		11.11		1	2.4
Holothuroidea														-19.31		18.03		1	4.4
Ocnus spp.	DF							-22.00		11.56		1	2.9						
Psolus fabricii	SF	-23.23		11.07		1	2.5												
BRYOZOA	SF	-20.13		10.36		1	2.3	-19.88		11.26		1	2.8						

Table 4. Ranged major axis (RMA) regression of benthic invertebrate stable carbon and nitrogen isotope ratios at Klondike, Burger, and Statoil.

Area	Intercept	Slope (β_{RMA})	p-value	95% Confidence Interval: Intercept	95% Confidence Interval: Slope
Klondike	44.55	1.69	0.01	(34.47, 61.07)	(1.17, 2.55)
Burger	47.29	1.83	0.01	(37.23, 62.82)	(1.30, 2.65)
Statoil	53.78	2.17	0.01	(42.08, 70.15)	(1.56, 3.01)

Table 5. Gross energy content (kJ g^{-1} DM, kJ g^{-1} WM) of selected benthic invertebrates. Values are reported as means with standard deviation (SD), and number of replicates (n).

Species/Taxon	KJ g^{-1} DM	SD	KJ g^{-1} WM	SD	n
CNIDARIA					
Stomphia spp.	16.18	1.78	2.16	0.23	2
SIPUNCULA					
Sipunculid	13.08	1.39	3.04	0.32	4
Golfingia margaritacea	10.20	2.42	2.33	0.55	4
PRIAPULA					
Priapulus caudatus	16.13	0.30	-	-	3
POLYCHAETA					
Flabelligeridae	21.47	0.91	-	-	2
Lumbrineris spp.	18.69	0.25	5.42	0.07	4
Maldanidae	10.20	4.47	3.41	0.06	3
Nephtys spp.	17.66	-	4.49	-	1
Paradiopatra parva	19.42	-	3.34	-	1
Paradiopatra spp.	23.35	-	5.58	-	1
Polynoidae	18.45	0.12	2.84	0.01	3
Terebellidae	13.72	0.31	3.6	0.08	4
MOLLUSCA					
Polyplacophora					
Ishnochiton albus	7.91	0.95	2.15	0.26	7
Gastropoda					
Buccinum polare	20.34	0.34	2.15	0.03	4
Buccinum scalariforme	20.85	1.53	2.21	0.16	10
Cryptonatica affinis	20.78	1.10	-	-	3
Euspira pallida	21.83	0.38	-	-	2
Margarites spp.	18.14	2.69	1.92	0.28	3
Neptunea spp.	21.27	0.22	-	-	2
Plicifusus spp.	18.65	0.32	7.49	0.13	3
Bivalvia					
Astarte borealis	21.85	-	0.74	-	1
Astarte montagui	18.38	0.15	0.62	0.01	2
Astarte spp.	21.14	0.05	0.71	0.01	2
Cyclocardia crebricostata	16.96	0.38	-	-	2
Ennucula tenuis	20.20	2.01	2.22	0.22	2
Macoma spp.	20.09	1.59	2.23	0.17	4
Nuculana radiata	15.29	7.30	0.98	0.47	2
Yoldia hyperborea	16.32	-	2.26	-	1
CRUSTACEA					
Amphipoda	24.18	-	7.47	-	1
Ampelisca spp.	28.12	-	11.41	-	1
Anonyx spp.	18.06	0.18	7.76	0.07	2
Stegocephalus spp.	17.44	0.53	5.19	0.15	3
Decapoda					
Argis lar	19.01	0.95	5.43	0.27	5
Chionoecetes opilio	13.67	0.88	4.97	0.32	3
Hippolytidae	15.21	0.90	-	-	6
Hyas coarctatus	8.16	0.43	2.58	0.13	2
Pagurus spp.	15.59	0.82	6.26	0.33	5
Pandalidae	19.25	0.78	-	-	2
ECHINODERMATA					
Asteroidea					
Ctenodiscus crispatus	6.82	0.38	-	-	3
Leptasterias groenlandica	8.27	3.42	3.06	1.26	3
Leptasterias spp.	12.71	1.14	4.55	0.41	3
Pteraster obscurus	10.51	2.34	-	-	2
Ophiuroidea					
Gorgonocephalus spp.	5.39	0.35	2.62	0.08	2
Ophiopholis aculeata	4.32	-	-	-	1
Ophiura sarsii	2.86	0.57	1.25	0.25	6
Holothuroidea					
Ocnus spp.	8.63	1.03	-	-	4
Psolus spp.	6.09	0.27	2.24	0.04	2
-	-	-	-	-	-

Table 6. Tukey multiple comparisons of mean gross energy density (kJ WM m^{-2}) among study areas Klondike, Burger, and Statoil following a significant ANOVA ($p = 0.01$). Values significant at $\alpha = 0.05$ are in bold.

Comparison	p-value
Klondike - Burger	**0.012**
Burger - Statoil	0.229
Klondike - Statoil	0.407

Table 7. Mean potential prey biomass and total biomass (g WM m^{-2}) by station, and proportion of total biomass accounted for by prey item biomass. Values are reported as means with standard deviation (SD) and are averaged over the 2009–2011 sampling period. Values based on Blanchard et al. (2013a, b), and Blanchard (unpublished data).

Klondike					
Station	Potential prey biomass (g WM m^{-2})	SD	Total biomass (g WM m^{-2})	SD	Potential prey/Total biomass proportion
KF001	193.02	17.57	200.91	129.53	0.96
KF003	138.08	18.41	171.33	55.34	0.81
KF005	161.20	14.14	299.42	185.87	0.54
KF007	102.44	9.08	159.32	45.22	0.64
KF009	165.44	18.99	198.86	13.41	0.83
KF011	160.30	34.14	248.88	130.12	0.64
KF013	203.28	16.82	224.56	19.89	0.91
KF015	50.37	3.44	160.14	150.58	0.31
KF017	109.34	27.39	184.16	74.43	0.59
KF019	86.31	6.86	119.35	49.72	0.72
KF021	98.89	20.43	116.86	-	0.85
KF023	156.99	17.50	199.54	36.00	0.79
KF025	205.85	26.42	297.02	39.80	0.69
Burger					
Station	Potential prey biomass (g WM m^{-2})	SD	Total biomass (g WM m^{-2})	SD	Potential prey/Total biomass proportion
BF001	106.71	13.94	203.00	5.69	0.53
BF003	209.68	18.10	311.71	85.00	0.67
BF005	268.14	18.79	416.76	46.85	0.64
BF007	353.67	51.61	412.32	157.97	0.86
BF009	183.57	13.55	394.63	19.63	0.47
BF011	271.33	20.01	471.35	166.60	0.58
BF013	280.77	24.94	444.57	128.66	0.63
BF015	386.23	40.00	548.31	224.69	0.70
BF017	188.82	15.69	408.41	97.64	0.46
BF019	261.39	29.76	392.77	58.81	0.67
BF021	225.62	29.05	367.09	133.19	0.61
BF023	196.23	29.55	308.66	50.79	0.64
BF025	338.19	52.49	349.97	68.76	0.97

Table 7. (*continued*)

Statoil					
Station	Potential prey biomass (g WM m^{-2})	SD	Total biomass (g WM m^{-2})	SD	Potential prey/Total biomass proportion
SF001	228.17	20.01	273.83	3.73	0.83
SF003	201.78	23.40	308.63	36.47	0.65
SF005	172.65	19.76	394.41	124.24	0.44
SF007	157.44	17.43	265.53	139.10	0.59
SF009	183.20	21.85	285.88	178.55	0.64
SF011	239.12	25.80	254.42	66.92	0.94
SF013	70.41	13.02	152.73	-	0.46
SF014	72.02	8.02	80.47	-	0.89
SF016	328.95	54.79	384.92	125.09	0.85
SF018	606.76	82.97	618.35	54.46	0.98
SF020	176.28	17.17	230.92	8.90	0.76
SF022	190.92	16.06	408.48	286.53	0.47
-	-	-	-	-	-